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**SCELETOMUSCULATURE AND SYSTEMATICS OF  
SCELIONIDAE  
(HYMENOPTERA: PLATYGASTROIDEA)**

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PhD dissertation

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TANAKAJD 2007**

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# INTRODUCTION

## OBJECTIVES

The insect order Hymenoptera encompasses approximately 10% of all known species on our planet, including such familiar and ubiquitous forms as the bees, ants, and wasps (LaSalle & Gauld 1993). This tremendous diversity is partitioned among three major groups: the aculeates, or stinging Hymenoptera; the sawflies or basal Hymenoptera (Vilhelmsen 2000a,b); and a number of taxa collectively referred to as the parasitic Hymenoptera. The Platygastroidea with two families, Scelionidae and Platygastriidae, is the third largest in between parasitic superfamilies, after Ichneumonoidea and Chalcidoidea, and comprising some 4460 described species worldwide (Johnson 1992).

The target group of the present dissertation is one of the families of Platygastroidea, the Scelionidae and concentrated on two major topics: i) functional morphology of Scelionidae and ii) the world revision of *Xenomerus* Walker genus (Hymenoptera: Platygastroidea: Scelionidae).

### 1. Functional morphology of Scelionidae

Morphological characters are important sources of data in systematics and taxonomic research, and an elaborate and arcane language has developed over the years to describe these features (e.g., Torre-Bueno 1989, Gordh & Headrick 2001). Unfortunately, the specialists in different taxonomic groups have often developed independent terminologies, resulting in numerous synonymies and a general barrier to effective communication. And even though the latest edition of the Torre-Bueno Glossary of Entomology numbers over 800 pages, for only English words, new and important morphological features are continually discovered, all of which need names. The intimate relationship between form and function and the correspondence of internal and external anatomy is well known and was amply demonstrated in even the early textbooks on insect morphology (e.g., Snodgrass 1935). External structures, such as sulci and pits, are often functionally correlated with internal scelotomuscular features. Proper recognition of homologies between structures, and of synonymies between terms, is facilitated by a consideration of features from both sides of the cuticular boundary.

This thesis is a contribution toward a comprehensive examination of the internal and external morphology of the insect family Scelionidae (Hymenoptera: Platygastroidea). One of the goals is to reconcile the different terms used in the taxonomic literature of this family of parasitoid wasps and to coordinate with the nomenclature used for other groups of

Hymenoptera. My thesis builds upon the recent important contributions of numerous authors, particularly those of Gibson (1985, 1986, 1993, 1997, 1999), Ronquist (1995), Ronquist & Nordlander (1989), and Vilhelmsen (1996, 1999, 2000a, 2000b, 2003).

I seek to provide a precise nomenclature for scelionid anatomy for use in systematics, and thus to contribute to further advances in our understanding of the taxonomy and interrelationships of its constituent groups. Given the enigmatic position of the family in the Apocrita (summarized in Austin et al. 2005), the recognition of homologous characters with other hymenopterans will facilitate work toward a robust phylogenetic hypothesis for the entire order.

## **2. World revision of *Xenomerus* Walker (Hymenoptera: Platygastroidea: Scelionidae)**

The subfamily Teleasinae (Platygastroidea: Scelionidae) is one of the most neglected groups of Platygastroidea. Although the monophily of the subfamily was demonstrated (Masner 1976, 1980; Austin & Field 1997; Austin et al. 2005), we have no information about its sister group relationship within Scelionidae, and its subfamily status is also questionable. With 466 species in 11 genera (Johnson 1992) Teleasinae is one of the largest and most common groups of Platygastroidea, however, the limits of genera within the subfamily are not well defined. This caused many problems in generic placement of new teleasine species, including *Xenomerus* species, recently described in *Trimorus* by Kononova & Kozlov (2001) and Kononova & Petrov (1999). One of the aims of the present thesis is to clarify the generic level concept of the genus *Xenomerus* on the basis of newly established morphological characters based on the correlation between external and internal structures such as internal apodemes, sceleto-musculature and gland systems (Mikó et al. 2007). Beside this, the author consider the present *Xenomerus* revision as a modell for further revisions in Hymenoptera; which should be based on the results of functional morphology first of all.

## HISTORICAL BACKGROUND

### SCELIONIDAE

The fossil record for Platygastroidea extends back into the Cretaceous, where scelionids are the most diverse group of Hymenoptera (Zherikhin & Sukacheva 1971). Specimens of scelionids and platygastriids are common in Baltic amber (Brues 1940), and many of these species belong to clearly recognizable modern genera. However, the relative distribution of these species among subfamilies is different. Almost all belong to the subfamily Scelioninae, while there are hardly any representatives of the subfamilies Teleasinae or Telenominae, both of which are abundant in numbers of individuals and species currently.

Scelionids are found in virtually all habitats except for the polar regions and are particularly diverse and abundant in the wet forests of the tropics and subtropics. Scelionidae are small, ranging in size from 0.5 to 12 mm in body length, but most are less than 2.5 mm. The great majority of species are morphologically simplified compared with other parasitic Hymenoptera, a trend that is largely size dependent. Most have greatly reduced wing venation, have the antennae inserted close together just above the mouth, lack a prepectus behind the lateral pronotum (typical of the Chalcidoidea), and, compared with many other microwasps, are well sclerotized and often intricately sculptured (Masner 1976, 1993, 1995).

All scelionid wasps are endoparasitoids in eggs of insects and spiders, and this is probably the ground plan biology for Platygastroidea. Although egg endoparasitism occurs in numerous groups of parasitic Hymenoptera, few family level taxa exclusively use eggs as hosts.

The only other families known for which this biology is characteristic belong to the Chalcidoidea, e.g., the Trichogrammatidae and Mymaridae (Huber 1986, Nagarkatti & Nagaraja 1977), and possibly the Mymarommatidae, whose biology is unknown.

Female scelionids have a hypodermic-like ovipositor that they use to pierce the chorion of a host egg (Austin 1983) and lay their own single egg or sometimes several eggs. The wasp larva that hatches consumes the contents of the host egg and pupates within it. A wide range of taxa serve as hosts. In addition to spiders, insect hosts include the Odonata, Orthoptera, Mantodea, Embiidina (= Embioptera), Hemiptera, Neuroptera, Coleoptera, Diptera, and Lepidoptera (Austin & Field 1997, Masner 1976). Many hosts of scelionids are pests of considerable importance in agriculture, forestry, and both human and animal health, e.g., the gypsy moth (*Lymantria dispar*), locusts (*Locusta migratoria*, *Choriocetes terminifera*), the sunn pest (*Eurygaster integriceps*), southern green stink bug (*Nezara viridula*), kissing bugs

(*Triatoma*, *Rhodnius*), and horse flies (*Tabanus* spp.). A number of species have been used as biological control agents with notable success (Clarke 1990, Drooz et al. 1977, Orr 1988, Bin 1994). Scelionids have also been important in the development of sex ratio theory (Hamilton 1964, Waage 1982, Colazza & Wajnberg 1998).

### **Relationships and monophyly of Platygastroidea**

Before 1970 the Scelionidae and Platygastriidae were mostly placed within the superfamily Proctotrupoidea, a taxon without unifying characters and have been served to accommodate a heterogeneous assemblage of apocritan families (Masner 1993, Naumann & Masner 1985). Masner (1956) was the first who considered Scelionidae and Platygastriidae as a superfamily separated from the Proctotrupoidea. This concept is now widely accepted by most hymenopteran systematists (Austin & Field 1997, Kononova & Kozlov 2001).

Despite the relative high number of recent phylogenetic studies based on molecular and morphological data for attempting to resolve the Apocrita phylogeny, the relationships of the Platygastroidea are still not clear. Analyses based on molecular data support a sister group relationship with Chalcidoidea (Dowton and Austin 2001), whereas available morphological data indicate a relationship with the Ceraphronoidea (Sharkey & Roy 2002), with Pelecinidae+Proctotrupidae+Vanhorniidae (Gibson 1999) and with Chalcidoidea (Ronquist et al. 1999).

The monophyly of the Platygastroidea was first proposed by Masner (1956). The evidence supporting this hypothesis comes primarily from two character systems: the modified structure of the abdomen in relation to the function of the ovipositor, and a unique sensilla on the female antenna. The dorsal and ventral plates of the abdominal segments of platygastroids are locked together (via laterotergites) and the spiracles of the tracheal system are reduced and nonfunctional. Together, these characters convert the abdomen into a pumping organ, used to generate high internal hydrostatic pressure for extrusion of the ovipositor (Masner & Huggert 1989, Austin & Field 1997). The apical segments of the female antenna are enlarged in size and generally referred to as a club or clava. The number of segments involved varies from 3-7, but on the underside of each of these segments, amidst the numerous tactile sensilla, are found one or two large multiporous basiconic sensilla (Bin 1981, Bin & Vinson 1986, Isidoro et al. 1996). The structure of these sense organs is unique in the Hymenoptera and also supports the monophyly of the group.

## **Classification, monophyly and phylogeny of Scelionidae**

The current higher-level classification for the Platygastroidea is partially based on the work of Kozlov (1970), who proposed a radical, though somewhat mechanistic, tribal classification for the two families. A large part of his scheme for the Scelionidae has been adopted in subsequent studies (Austin & Field 1997, Galloway & Austin 1984, Masner 1976), but with a number of significant modifications, e.g. incorporation of Baeinae into Scelioninae.

Although the monophyly of Platygastroidea is undisputed and Platygastriidae is putatively a well-supported group, recent works based both on molecular and morphological data suggest that Scelionidae is not a natural group (Austin & Field 1997, Gauld & Bolton 1996, Manser & Huggert 1989, Austin et al. 2005, Dowton & Austin 2001), furthermore, there is no appreciable diagnostic character for the family.

Relationships at lower taxonomic levels are also problematic. Austin & Field (1997) concluded that the largest subfamily, Scelioninae, is defined only by symplesiomorphies and is probably paraphyletic, while the Teleasinae, Telenominae, and many tribes probably represent natural assemblages, although many of them are not supported morphologically.

Of all characters recently examined, the ovipositor system has been the most useful for inferring putative relationships (Austin & Field 1997, Austin et al. 2005).

Little work has been undertaken on the phylogeny of individual tribes (Embidobiini and Baeini) (Austin & Field 1984), and genera, *Scelio* (Dangerfield, Austin & Baker 2001), *Psix* (Johnson & Masner 1985), *Trissolcus* (Johnson 1984). In addition to these studies, differences among character states associated with the ovipositor system and associated structures have led to questioning the monophyly of numerous large genera (e.g., *Anteris*, *Ceratobaeus*, *Idris*, *Opisthacantha*, *Telenomus*, *Trimorus*, and *Platygaster*) (Austin & Field 1997, Iqbal & Austin 2000).

## **Species richness**

Presently there are 3308 valid species of Scelionidae (Johnson 1992), with only 15 genera recorded with more than 50 described species: i.e., *Telenomus* (612 spp.), *Platygaster* (419 spp.), *Trimorus* (389 spp.), *Gryon* (273 spp.), *Scelio* (246 spp.), *Trissolcus* (170 spp.), *Synopeas* (166 spp.), *Ceratobaeus* (161 spp.), *Idris* (145 spp.), *Sparasion* (140 spp.), *Macroteleia* (128 spp.), *Baryconus* (69 spp.), and *Calliscelio* (60 spp.).

## Biology

The most detailed biological studies have been undertaken on scelionids that are used as or have potential as biological control agents (Bin & Johnson 1982).

Host finding and acceptance in the Telenominae and *Gryonini* appears to be largely influenced by kairomones on the eggs and presumably plant synomones (Mattiacci et al. 1993, Strand & Vinson 1993), while Baeini appears to search first for the bark of trees and then for the silk of their spider host (Austin 1984). The mechanism of host finding for scelionids that parasitize host eggs in soil such as Teleasinae is unknown and may be mediated by chemical residues from host oviposition or changes in the texture of the soil surface (Austin et al. 2005, Mikó et al. 2005). Phoresy has been recorded for species of *Sceliocerdo* and *Synoditella* associated with acridid hosts; *Mantibaria* of mantids; *Thoronella* on Odonata; *Epigryon*, *Protelenomus*, and *Telenomus* associated with Heteroptera; and *Telenomus* on Lepidoptera (Dangerfield et al. 2001, Masner 1995).

Scelionids are virtually all solitary idiobiont primary parasitoids, and reports that diverge from this biology are rare and often unsubstantiated (Austin et al. 2005).

Many species exploit hosts that lay clumped batches of eggs and adaptations to prevent superparasitism are common. Usually females mark host eggs either externally or internally (Eberhard 1975). External or internal chemical marks are applied via the ovipositor (Eberhard 1975, Wilson 1961). External marks are recognized by sensilla on the antenna and internal marks are probably more common and largely detected by ovipositor sensilla (Austin et al. 2005). Host eggs are not suitable for all of their embryonic period, and successful oviposition occurs mostly in the early stages (Vinson 1994). Parasitized host eggs change color at some stage during development, usually becoming much darker than unparasitized eggs.

## FUNCTIONAL MORPHOLOGY

Data on Hymenoptera functional morphology was provided in papers on comparative anatomy of different insect orders (Crampton 1909, 1914, 1919a, 1919b, 1920a, Snodgrass 1935, Maki 1938, Bradley 1939, Pringle 1957, Matsuda 1970). These studies are crucial in term of understanding different biological mechanism (e.g., mechanisms of flight or copulation) and their evolution within Insecta. In these studies, authors rarely provide original descriptions of specific body parts of some Aculeata and Symphita species, and mostly used available descriptions for strengthening their theories.

However, in a number of studies, detailed descriptions of the scelotomusculature of hymenopteran species are given (*Apis mellifera*: Snodgrass 1910; *Vespa pensylvanica*:

Duncan 1939; *Stenobracon deesae*: Alam 1951; *Athalia proxima*: Dhillon 1966; *Camponotus camelinus* Saini et al. 1982). Besides the detailed descriptions of the sceleotomusculature, the authors also try to explain the mechanisms of flight, walking and copulation; in some cases proposed theories concerning the evolution of different character systems within Hymenoptera (e.g., evolution of the axillary level within Apoidea: Snodgras 1942) or discussed the intraspecific variability of thoracic muscles (Saini et al. 1982).

Daly (1963) and Shcherbakov (1980, 1981) provided the first comparative studies of morphology with phylogenetic implications on Hymenoptera. Their works based partly on their own observations on the sceleotomusculature of the thorax and partly on the summarizing of previous studies on functional morphology.

Early students of Hymenoptera phylogeny (Oeser 1961, Brothers 1975, Königsmann 1976, 1977, 1978a, b; Rasnitsyn 1980) mostly worked with compiled data from the descriptive taxonomy, without consideration of corresponding internal characters or the results of functional morphology research.

Because morphologists and taxonomists worked separately, they developed different character systems and hence there were many discrepancies in character states, interpretation of homologies and first of all in terms used for sceletal structures.

Gibson (1985) tried to correct and standardize the inconsistent and multiple use of some morphological terms for external structures on the basis of functional morphology and hence to bridge the gap between functional morphology and systematics. Most of the subsequent students of Hymenoptera functional morphology (Saini 1986; Johnson 1988; Whitfield & Johnson 1989; Ronquist & Nordlander 1989; Danforth 1989; Quicke & Fitton 1992; Quicke & Fitton 1992; Gibson 1993; Heraty et al. 1994; Vilhelmsen 1997, 2000a,b,c; Schulmeister 2003a) followed Gibson's concept, solving discrepancies between functional morphology and systematics.

Rasnytsin (1988) proposed the first phylogenetic analysis of Hymenoptera involving the results of earlier functional morphology research. However, his phylogenetic hypothesis is narrative and not based on an explicit cladistic analysis. The morphological character matrix for Hymenoptera given by Ronquist et al. (1999) was the first cladistic analysis which encompassed most of the families in the order. Basically they used the same character set given by Rasnitsyn (1988) earlier, however, with a cladistic approach. Recently, Sharkey & Roy (2002) proposed a cladistic analysis of Hymenoptera which was in fact a re-analysis of Ronquist et al. (1999), with some additional wing venation characters.

These papers could be considered as landmarks for further phylogenetic research, however, the generated data matrices included mostly combined data and missed many characters peculiar for the apocritan taxa.

Vilhelmsen (2001) gave the first cladistic analysis of basal Hymenoptera involving the entire sceleptomusculature of the thorax.

The molecular analysis have played an increasingly important role in the phylogenetic research of Hymenoptera (Cameron 1991, 1993; Derr et al. 1992; Baur et al. 1993; Dowton & Austin 1994; Dowton et al. 1997; Belshaw et al. 1998) by the end of the 20<sup>th</sup> century. Although initially molecular data were often used to address problem areas in morphological phylogenies, presently increasing attention is paid to the congruence between morphological and molecular results (Carpenter & Wheeler 1999, Dowton & Austin 2001, Schulmeister et al. 2002, Schulmeister 2003b).

Recent phylogenetic analyses either combined or use only morphological characters, try to involve the results of the functional morphology, however, many of the character states are unknown for a number of higher taxa, particularly in parasitic Hymenoptera. For robust and correct phylogenetic analysis it is therefore necessary to determine more accurately the distribution and homology of these character states in all higher taxa, including Platygastroidea.

## **MATERIALS AND METHODS**

### **INSECT MATERIAL**

#### **Morphology of Scelionidae**

Members of 25 scelionid genera were examined. Most of the examined specimens were obtained from the collection of the Systematic Parasitoid Laboratory (Kőszeg, Hungary); specimens of *Nixonia* were provided by N.F. Johnson (Columbus University, Columbus, Ohio, USA); *Archaeoteleia* and *Calliscelio* from Chile by J. Heraty (University of California, Riverside, USA); *Tiphodytes* by F. Bin (Università di Perugia, Italy). The non-scelionid Hymenoptera specimens were donated primarily by L. Vilhelmsen (Natural History Museum, Copenhagen, Denmark); specimens of *Proctotrupes*, *Helorus*, *Andricus*, *Belyta*, *Trichopria*, *Isocybus*, *Trichacis* and *Inostemma* are coming from the collection of the Systematic Parasitoid Laboratory. A list of examined species with locations is given in APPENDIX 2. The number of specimens examined is given in parenthesis following species names.

#### **World revision of *Xenomerus***

430 *Xenomerus* specimens were loaned for examination from 13 institutions worldwide (APPENDIX 3).

### **TECHNIQUES**

Dissections for examination of muscles were based on specimens preserved in 70% ethanol. All specimens were transferred to 96% ethanol and critical-point dried. The specimens were transferred to Blu Tack (Bostik Findley 2001) and dissected with insect pins (size: 000) or minutens. For examination of pleural muscles, specimens were halved with a razor blade. Almost all of the muscles were removed from the body parts during dissections. The remnants of the specimens are deposited in the collection of the Systematic Parasitoid Laboratory (Kőszeg, Hungary).

Dissections for skeletal structures were based on dried or ethanol-preserved specimens. The dissected specimens were macerated in KOH and transferred to 96% ethanol. Part of the series was critical-point dried and examined with SEM and part was transferred to clove oil and examined under stereo (Leica MZ6) and phase-contrast (Olympus BH2) microscopes. Critical-point dried and dissected specimens were mounted with double adhesive tape on stubs and coated with gold prior to SEM examination.

Critical-point dried and dissected specimens were transferred to Blu Tack for digital

imaging. Digital images were taken with a Nikon Coolpix 4500 camera attached to an Olympus BH2 phase-contrast microscope. To avoid glare and light reflections, a sheet of tracing paper was used to disperse light. A series of photographs were prepared by focusing on different levels of the structure and these combined by CombineZ5 (Hadley 2006) using “do combine” and “do average and filter” commands. Images were processed in Adobe Photoshop 6.0. Linear drawings were made in Adobe Photoshop 6.0 based on dissected specimens, stored in clove oil and examined under the stereomicroscope.

Whole mounts were observed under transmitted light through a semitransparent sheet (Mylar tracing paper) to eliminate excess glare. General observations were made by the stereo binocular (Leica MZ6) at 160× magnification. Acrosternal calyx of S5, ovipositor system and wing venation were studied on slide mounts embedded in Canada balsam (Prinsloo 1980).

## **TERMINOLOGY**

### **Morphology of Scelionidae**

The terms propectus, mesopectus, and metapectus are used to refer to fused pleural and sternal components of the thoracic segments. Terms for skeletal structures generally follow Masner (1980), Ronquist & Nordlander (1989), and Vilhelmsen (2000a, b). Additional terms are derived from Bin & Dessart (1983), Duncan (1939), Gibson (1985, 1986, 1997), Gordh & Headrick (2001), Heraty et al. (1994), Huber & Sharkey (1993), Johnson (1984, 1996), Johnson & Masner (1985), Masner (1972, 1979a, b, 1983, 1991), Ronquist (1995), Snodgrass (1942), Vilhelmsen (1999), and Yoder (2004).

Terms referring to skeletal structures appear in bold face the first time they occur in the text. Abbreviations and figure references are given in parenthesis following the term. Abbreviations, the reference to works where the terms were defined or redefined and proposed, and synonyms are given in APPENDIX 4. New or modified terms are denoted with an asterisk (\*).

We generally do not use names for muscles that refer to their function, because the function may be ambiguous, difficult to discern, may differ among taxa, or different muscles may have the same function in different taxa. Instead, we follow Vilhelmsen (1996, 2000a, b) and refer to muscles as follows: the first component of the name refers the site of origin, the second component to the site of insertion of the muscle. Suffixes may be used to indicate the relative position of muscles with the same origin and insertion. Muscles usually have a fan-shaped origin and insert on a tendon. If the muscle is rodlike, i.e., attaching with tendons at both site of origin and insertion, then its site of origin is based on its function. For example, the

third mesopleuro-mesonotal muscle is a retractor of the mesoscutum; therefore its site of origin is the mesopleuron and its site of insertion is the mesoscutum. Terms referring to muscles appear in bold and italics the first time they occur in the text. Figure references are given in parentheses following the term. The terms for muscles used in the present paper, figure references, function and possible homologies are given in APPENDIX 5.

### **World revision of *Xenomerus***

Terms for skeletal features, concerning head and thorax, follow Mikó et al. (2007a). Surface-sculpture terminology follow Harris (1979), terminology of wing venation Masner (1980) and ovipositor assemblages Austin & Field (1997). List of additional characters is listed below (new or modified characters are marked with\*):

**A1-A11(A12):** antennomeres

**Clava:** (**clava:** Fig. 175; Bin 1981): The clava consist of the six apical antennomeres (clavomeres) in female Teleasinae bearing multiporous gustatory sensillae (MGS, Isidoro et. al 1996, 2001).

**Claval formula** (Bin 1981): Ratio of number of MGS on clavomeres from A7-A12.

**Erect bristle of male antennomere** (**es:** Fig. 169; Masner 1980): elongated, erect or semi-erect bristles located in whorls on the widest part of male antennomeres. The erect bristles might be homologues with *sickle shaped sensillum* of *Trisolcus basalis* (Bin et al. 1989) and *Type 3 sensilla* of *Entomacis* (Yoder 2004).

**Ventral microcilia\*** (**vm:** Figs 169, 170, 172): ventrally located seta on male antennomeres much shorter than erect bristles. Ventral microcilia might be homologous with *sensillum chaeticum* or *sensillum* or *sensillum conicum* of *Trisolcus basalis* (Bin et al. 1989) and *Type 2 sensilla* of *Entomacis* (Yoder 2004).

**Lateral and inter notaular areas\*** (**LNA, INA:** Fig. 160): areas on the mesoscutum, separated by the notaulus.

**Anterior and posterior rows of foveae of mesopleural carina\*** (**arf, prf:** Fig. 238): rows of foveae extending anterior and posterior to the mesopleural carina.

**T1-T6 (T1-T6:** Fig. 166; Austin & Field 1997): metasomal terga corresponding to abdominal terga 2-7 (A2-A7: Austin and Field 1997).

**Apical setae on T3\*** (**asT3:** Fig. 166): ordered setae in transverse row close to the posterior margin of T3.

**T7+8** (**T7+8**: Fig. 166; Austin & Field 1997): metasomal tergum corresponding with fused abdominal terga 9 and 10. **Cerci** (**cr**: Fig. 166) and **apical setae on T7+8\*** (**asT7+8**: Fig. 166) are located on the dorsal surface of T7+8.

**Lateral setae on T1\*** (**lsT1**: Fig. 166): setae located laterally on T1. Lateral setae on T1 might be homologous with *mid petiol setae* of *Entomacis* (Yoder 2004).

**Basal grooves on T1, T2 and T3\*** (**bsgT2,3**: Fig. 166): ordered grooves located along the anterior margin of T1, T2 and T3, from which costae can be developed.

**Lateral patch of T2-T6\*** (**lpT2-T6**: Fig. 166): coriaceous, setaceous, elongate patch extending along the lateral margin of T2. The lateral patch of T2 could be homologous with the *anterior pits on T2* in Platygasteridae (Masner & Huggert 1989). The lateral patch corresponds with the tergo-sternal muscles of each metasomal segments.

**Posterodorsal patch of T3\*** (**pdpT3**: Fig. 166): coriaceous and setaceous patch with a median pore like opening on the posterolateral part of T3.

**Median patch on T4\*** (**mpT4**: Fig. 166): coriaceous and setaceous patch located submedially on T4.

**S1-S6** (**S1-S6**: Fig. 165; Austin & Field 1997): metasomal sterna corresponding with abdominal sterna 2-9 (A2-A9: Austin & Field 1997).

**Basal grooves on S1, S2 and S3\*** (**bsgS2,3**: Fig. 165): ordered grooves located along the anterior margin of S1, S2 and S3, from which costae can be developed.

**Lateral inflection of S2-S6\*** (**liS2**: Fig. 165) inflections along the lateral margins of metasomal sterna 2-6, marking sites of origin of **laterosterna** (**LS2-5**: Fig. 5; Masner 1976, 1980).

**Anterior pit of S2** (**atS2**: Fig. 165; Masner & Huggert 1989): pit on the anterolateral edge of S2 medially of the lateral inflection of S2. The *anterior pit of S2* corresponds with an internal apodeme (**ina**: Fig. 168).

**Felt field** (**ff**: Fig. 165; Masner & Huggert 1989): coriaceous, setaceous, elongate patch laterally on S2 posterior to the *anterior pit* of S2 with a median pore like opening.

**Posterior felt field\*** (**pff**: Figs 165, 167): coriaceous and setaceous patch with median pore like opening (**mpo**: Fig. 167) on S3 in males. The felt field and posterior felt field correspond internally to tubular structures (**tst**: Fig. 168) similar to the secretory cell ductules of many Braconidae (Buckingham & Sharkey 1988).

Whether the coriaceous sculpture and median opening of posterodorsal patch of T3, felt field and posterior felt field are secondary cuticle modifications related to Type III. exocrine glands (Noirot & Quenedey 1972) requires more detail examination of the metasoma using

TEM techniques.

**Retractors of metasomal sterna S2-S6\*** (**S3-S2**: Fig. 168; **S4-S5**: Figs 279-280) The fan shaped external retractor of the metasomal sternum originates from the posterior part of the preceding sternum and inserts to the anterior margin of its acrosternite. The muscle is most elongated and expressed between S4 and S5 in Teleasinae and could be homologous with muscle 164 of *Apis* (Snodgrass 1942) and muscle *misr* of *Vespula* (Duncan 1939).

**Acrosternal calyx of S5\*** (**acS5**: Figs 165, 279-281): median, paired, calyx like depression on the weakly sclerotized acrosternite on of S5. The acrosternal calyx of S5 is well developed in Teleasinae, *Anteris* and *Tiphodytes*. The enlarged retractor of S5 inserts to the anterior margin of the acrosternite, just anterior to the acrosternal calyx. We found two circular, sac-like structures in some teleasines which were not macerated in KOH. These structures seem to be intact secretory cells connecting to the acrosternal calyx. The external surface of the *acrosternal calyx* is usually covered by the 4<sup>th</sup> sternum.

We assume, that the acrosternal calyx of S5 could serve as a secondary reservoir for type III gland cells. Acrosternal calyx closure could be result from the contraction of the acrosternal muscles, while opening might be result from the change of hydrostatic pressure of the hemolymph (Austin & Field 1997, Austin et al. 2005) during oviposition. Similar gland reservoirs and opening mechanisms were described by Buckingham and Sharkey (1988) in Agathidinae (Braconidae) and by Van der Vecht (1968) in Vespidae. The function of acrosternal calyx and the putative exocrine gland is unknown.

Descriptions of different character states used in keys and species descriptions are explained and figured in the generic description of *Xenomeres* (see below).

## MEASUREMENTS

Body length was measured from the apex of interantennal process to the tip of the metasoma and is provided only as a general indication of size. Most of the following measurements follow Johnson (1984), Masner (1980) new measurements are marked with\*. We measured the length of marginal vein between the first marginal placoid sensilla and distal end, because it is nearly impossible to locate the exact border between premarginal and marginal veins. Head width (**HW**), head length (**HL**), head high (**HH**), inter orbital space (**IOS**), posterior ocellar line (**POL**), ocular ocellar line (**OOL**), lateral ocellar line (**LOL**), length of radicle (**r**), length of A1 (**A1**), length of clava (**clava**), transscutal line (**TSL**)\*, maximum length of mesoscutum (**ML**), maximum length of mesoscutellum (**SL**), distance between posterior end of notauli (**DPN**)\*, distance between posterior end of notaulus and

posterolateral edge of mesoscutum (**DNP**)\*, mesoscutellum width between axillular carinae (**SW**)\*, length of marginal vein between anterior placoid sensilla and posterior end of marginal vein (**m**)\*, length of stigmal vein (**st**), maximum length of metasomal terga (**T1L, T2L, T3L**), maximal width of metasomal terga (**T1W, T3W**(maximum with of T2) were taken as indicated in Figures: 161-164 and 166. The ratio **FCI** (frontal cephalic index) means the ratio of HW/HH, the ratio **LCI** (lateral cephalic index) means the ratio of HH/HL. In descriptions the maximum and minimum values, mean (M=) and standard deviance (SD=) of ratios are given.

## DESCRIPTIONS

Species were described from holotypes, except *X. ergenna*, *X. canariensis*, *X. varipes* and *X. laticeps*, where types were not available or they were in a very bad condition for measuring metrics. Species descriptions are for the most part comparable, character states are presented in sequence of body parts. For a few species, additional features (*e.g.*, distance between posterior end of notauli in *ergenna*-group, completeness of toruli triangle in *X. noyesi* and *X. fulleri*, presence of keel extending between anterior margin of mesoscutellum and scutellar spine and ratios A3/A4 and A3/A2 in *X. spinosus* and *X. armatus*) are described that are not mentioned in other species descriptions. These features are absent or do not vary diagnostically in form for species in which they are not mentioned. Features in the diagnoses are presented in order of importance. Specimens not involved in type series are listed as other material examined.

## RESULTS AND DISCUSSION

### MORPHOLOGY OF SCELIONIDAE

#### Results

##### *Head*

*Skeletal structures.* The **vertex** (**vrx**: Fig. 2) is the dorsal part of the head between the level of the dorsal margin of the **occipital carina** (**occ**: Figs 2, 30, 32, 33) and the level of the ventral margin of the **anterior ocellus** (**aoc**: Fig. 1b). The anterior ocellus and the **lateral ocelli** (**loc**: Fig. 1b) delimit the triangular **interocellar space** (**ics**: Fig. 1b) on the vertex. The **hyperoccipital carina** (**hyc**: Fig. 2) crosses the vertex and extends just posterior to the lateral ocellus in some Scelionidae. The **vertex patch\*** (**vpt**: Fig. 1a) is on the vertex between the lateral ocellus and the inner margin of the eye.

The **frons** (**fro**: Fig. 1a) is the anterior surface of the head between the level of the ventral margin of the anterior ocellus and the dorsal margin of the **antennal foramen** (**anfo**: Fig. 1). The unpaired **preocellar pit** (**prp**: Figs 1a, 20) is just ventral of the anterior ocellus in some Telenominae and corresponds internally with a cup or bell-shaped apodeme. The **frontal ledge** (**fld**: Fig. 21) crosses the dorsal part of the frons in *Sparasion*, *Acanthoscelio*, *Breviscelio*, *Tyrannoscelio*, and *Encyrtoscelio*, separating a vertical and a horizontal area. The **orbital band** (**obb**: Fig. 22) is a vertically elongated reticulate area along the inner orbit of the eye in Telenominae. In Teleasinae, a coriaceous **frontal patch\*** (**frp**: Figs 1a, 23) occurs near the inner orbit. The longitudinal **central keel** (**ctk**: Figs 1a, 23, 25) extends between the anterior ocellus and the **interantennal process** (**iap**: Figs 1a, 20, 21, 23, 25, 26) in some Scelionidae. The central keel bifurcates ventrally to surround the antennal foramen, thereby delimiting the usually setaceous **torular triangle\*** (**trt**: Figs 1a, 23, 25) or extends to the interantennal process without bifurcating. The **antennal scrobe** (**asc**: Figs 1a, 23) is a smooth area lateral of the central keel. In some Scelionidae the frons has a more or less well-developed **frontal depression** (**fdp**: Figs 22, 24), which in *Baryconus* and some members of the *Psix*-group of genera of Telenominae is limited laterally by the **submedian carina** (**sbc**: Figs 1a, 24). The interantennal process is situated ventrally on the frons and laterally bears the antennal foramen in most Scelionidae, but is absent from *Nixonia*.

The **malar region** (**mlr**: Fig. 1a) is the ventrolateral part of the anterior surface of the head limited laterally by the lower orbit of the eye and the **malar sulcus** (**mas**: Figs 1a, 23, 25). The malar sulcus extends between the lower orbit and the base of the mandible. The **facial**

**striae\*** (**fas**: Figs 1a, 23, 25) radiate from the base of the **mandible** (**mdb**: Figs 1a, 21, 156, 157) onto the malar region. Some of the facial striae extend to the frons and vertex along the inner orbit. The **orbital carina** (**obc**: Figs 1a, 25), present in *Psix*, extends from the base of the mandible along the inner orbit.

The externally convex **clypeus** (**cly**: Figs 1a, 23, 25) is ventral to the interantennal process. The anterior margin of the **oral foramen** (**orf**: Fig. 1b) lateral to the clypeus is impressed to the **pleurostomal condyle** (**pscy**: Figs 1b, 26, 28) and serves as the anterior mandibular articulation. It is usually polished and fused to the ventral surface of the anterior part of the **tentorium** (**tntr**: Figs 1b, 27, 29). The tentorium is vertically flattened anteriorly and corresponds externally with the **anterior tentorial pit** (**atp**: Fig. 28), which is lateral to the clypeus just dorsal to the impressed margin of the oral foramen in *Sparasion* and some Telenominae (Bin & Dessart 1983), but is absent from other Scelionidae.

Internally, the **epistomal ridge** (**epsr**: Figs 1b, 34) and the **vertical ridge of the clypeus\*** (**vrcl**: Figs 1b, 34) extend from the pleurostomal condyle medially. The epistomal ridge bifurcates before reaching the antennal foramen, with a dorsal branch extending just medial of the antennal foramen and a vertical branch delimiting the clypeus internally. The two dorsal branches and the vertical branch delimit an internally concave area that corresponds externally with the interantennal process. The vertical ridge of the clypeus serves as the site of attachment of the **labrum** (**lbr**: Figs 1b, 26). The weakly sclerotized labrum is usually concealed by the clypeus. The number of **labral setae** (**lbrs**: Figs 1a, 26) along the ventral margin of the labium varies in Scelionidae. The **pleurostomal ridge** (**plsr**: Figs 1b, 34) extends from the pleurostomal condyle along the lateral margin of the oral foramen to the **pleurostomal fossa** (**plsf**: Figs 2, 26, 28), which serves as the posterior mandibular articulation. The pleurostomal fossa is on the posterior margin of the oral foramen in most Scelionidae (Fig. 26). In *Sparasion*, the pleurostomal fossa is on the lateral margin of the oral foramen (Fig. 28). The **hypostoma** (**hy**: Figs 2, 31) is posterior to the pleurostomal fossa and is limited dorsally by the **hypostomal sulcus** (**hys**: Figs 2, 30, 31). The margin of the oral foramen is produced into a **hypostomal tooth\*** (**hyst**: Figs 2, 30, 32) at the junction of the hypostoma and the pleurostomal fossa. The inflected hypostoma serves as the site of articulation of the **maxilla** (**maxl**: Figs 2, 30–32). The stipes is the only part of the maxilla visible externally; the reduced cardo is hidden by the **postgenal bridge** (**pgb**: Figs 2, 30–32). The postgenal bridge is the median part of the **postgena** (**pg**: Fig. 2) between the **occipital foramen** (**ocf**: Figs 2, 30, 32) and the hypostomal sulcus. The usually setaceous **median sulcus of the postgenal bridge\*** (**mspb**: Figs 2, 31) is situated in the middle of the postgenal bridge in

most Scelionidae. The **postgenal sulcus\*** (**pos**: Figs 2, 30, 32) laterally delimits the postgenal bridge in some Scelionidae. The tentorium fuses posteriorly with the postgenal bridge lateral to the occipital foramen. A posteriorly widened **ventral lamella\*** (**vla**: Figs 1b, 27, 29) arises ventrally from the median part of the tentorium. The **postgenal pit\*** (**pgp**: Figs 2, 30, 32) corresponds with the ventralmost point of the posterior site of fusion of the ventral lamella. The **tentorial bridge** (**tbr**: Figs 2, 29) originates just medially of the posterior end of the tentorium and corresponds with the **posterior tentorial pit** (**ptp**: Figs 1b, 2, 30, 32).

The distance between the posterior tentorial and postgenal pits varies in Scelionidae. In most cases the postgenal pit is in or just ventral to the **fossa** (**fos**: Figs 2, 30, 31, 32), much closer to the occipital foramen than to the oral foramen (Fig. 30). In some species of *Gryon*, *Eremioscelio*, *Encyrtoscelio*, *Breviscelio*, *Dyscritobaeus*, and in some Teleasinae (Fig. 32), the postgenal pit is closer to the oral foramen than to the occipital foramen.

The **postocciput** (**posu**: Fig. 2) surrounds the occipital foramen; the fossa is the circular depression surrounding the postocciput. The **occipital condyle** (**ocy**: Figs 2, 30–32) is located ventrolaterally on the postocciput and articulates with the **cervical prominence** (**cvpr**: Figs 4, 5, 16, 35) of the prothorax. The occipital carina is an inverted U-shaped carina that extends from the oral foramen dorsal to the occipital foramen and that delimits a ventral area on the posterior surface of the head (Fig. 2). The **occiput** (**ocp**: Fig. 2) is limited dorsally by the occipital carina and ventrally by the occipital foramen. The **gena** (**gen**: Figs 1a, 2) is the posterolateral area of the head limited laterally by the outer orbit and the malar sulcus and medially by the occipital carina. Dorsally, the gena extends to the level of the dorsal margin of the occipital foramen. The **genal patch\*** (**gnp**: Figs 2, 30) is a small area of fine sculpture on the dorsal part of the gena.

*Muscles.* The posterior cranio-mandibular muscle is the largest muscle in the head, having several muscle bands that insert on the **mandibular adductor muscle apodeme** (**maa**: Figs 2, 21). The posterior margin of the site of origin of the **median band of the posterior cranio-mandibular muscle** (**cr-mdpm**: Figs 2, 21, 29, 33) corresponds externally with the median part of the occipital carina, whereas the lateral part of occipital carina crosses the origins of the **lateral bands of posterior cranio-mandibular muscle** (**cr-mdpl**: Figs 2, 21). The anterior extension of the lateral bands of the posterior cranio-mandibular muscle varies in Scelionidae. In some cases some anterior bands extend to the frons (*Scelio*, *Gryon*, *Trissolcus*) and to the interocellar space. The anterior margin of the site of origin of the median band of the posterior cranio-mandibular muscle corresponds externally with the hyperoccipital carina. In *Archaeoteleia*, the **anterior cranio-mandibular muscle** (**cr-mdp**: Figs 1a, 21, 34) originates

entirely from the internal surface of the gena, and the malar region serves as the site of origin of the *cranio-antennal muscle* (*cr-A1*: Figs 1a, 21, 34). The border between the sites of origin of the anterior cranio-mandibular muscle and the cranio-antennal muscle corresponds externally to the malar sulcus. In other Scelionidae the site of origin of the anterior cranio-mandibular muscle extends distinctly anteriorly of the malar sulcus. The dorsal extension of the site of origin of the anterior cranio-mandibular muscle and cranio-antennal muscle and the corresponding external structures vary in Scelionidae. In some Teleasinae and the *Psix* group of genera of Telenominae, the attachment sites of the muscles extend towards the midlevel of the eye and correspond with the dorsally extended facial striae along the inner orbit (Fig. 25). In the *Psix* group of genera the orbital carina corresponds to the border between the anterior cranio-mandibular muscle and cranio-antennal muscle. The site of origin of the anterior cranio-mandibular muscle corresponds with the orbital band in Telenominae and the frontal patch in Teleasinae. The anterior cranio-mandibular muscle extends to the top of the head and originates partly from the horizontal area of the frons delimited by the frontal ledge in *Sparasion* (Fig. 21). The *cranio-pharyngeal plate muscle* (*cr-phr*: Figs 1a, 34) originates from the frons above the antennal foramina. The size of the muscle varies and usually is enlarged in taxa having a well developed frontal depression. The *tentorio-antennal muscle* originates from the dorsal surface of the anterior broadened part of the tentorium, and the *tentorio-labial* and *tentorio-stipital muscles* from the ventral surface.

#### *Propleuron, prosternum and profurca*

*Skeletal structures.* The propleuron and prosternum are connected to the pronotum and mesopectus (mesopleuron + mesosternum) by extensive membranous areas, which provide for a high degree of motility.

The site of fusion of the cervical prominence corresponds with the **propleural cervical sulcus\*** (*pcs*: Figs 3, 16, 19, 35, 36), which extends along the anterodorsal margin of the ventral propleural area. The cervical prominence articulates with the occipital condyle. The **cervical apodeme** (*crva*: Figs 4, 5, 42, 44, 46) is the posterior extension of the cervical prominence and is fused with the dorsal part of the propleuron.

The **longitudinal carina of the propleuron\*** (*lcp*: Figs 3, 36) separates the **ventral\*** and the **lateral propleural areas\*** (*vpa*, *lpal*: Figs 3, 5, 6, 36). The weakly sclerotized **dorsal propleural area\*** (*dpl*: Figs 3, 5, 40) is posterodorsal of the well-sclerotized lateral propleural area and usually differs from it in sculpture. The reduced **propleural arm** (*ppa*: Figs 3, 40, 41) is on the posteroventral corner of the dorsal propleural area. The dorsal propleural area is

usually smooth externally, which may allow for free movement between it and the pronotum. The **propleural epicoxal sulcus\*** (**pes**: Figs 3, 16, 19, 35) sets off the **epicoxal lobe\*** (**epl**: Figs 3, 16, 19, 35) from the ventral part of the ventral propleural area. The **lateral articular process** (**lapr**: Figs 5, 6, 37) for the procoxa lies anterolaterally on the ventral margin of the propleuron. The **ventral edge of the propleuron\*** (**vgp**: Figs 5, 6, 35, 37) sets off the **ventral vertical lobe of the propleuron\*** (**vv1**: Figs 5, 6, 37, 38, 41, 45), which is inflected 90° relative the ventral propleural area.

The prosternum is divided into two parts: the well sclerotized, externally visible **basisternum** (**bstr**: Figs 4–6, 37, 38, 41, 45) and the weakly sclerotized **furcasternum** (**fust**: Figs 4–6, 37, 41, 45), which is concealed by the **ventral bridge of the pronotum** (**vbp**: Figs 7, 16, 35, 49, 50, 56, 57, 59–61). The basisternum and furcasternum are almost entirely separated by the deep, transverse **prosternal incisions\*** (**psin**: Figs 5, 6, 37, 38, 41, 45), only being continuous for a short distance medially. The **lateral basisternal projection\*** (**lbp**: Figs 4–6, 37, 38, 41, 45) extends anterolaterally and forms the **median articular process** for the procoxa. The **anterior process of the prosternum\*** (**app**: Figs 5, 6, 35, 37, 45) fits into the incision between the ventral vertical lobes. The **profurcal arms** (**fu1a**: Figs 3, 5, 6, 40, 41, 45) originate medially from the furcasternum and correspond to the externally separated **profurcal pits** (**prfp**: Figs 6, 37, 38, 41, 45). The profurcal arm articulates laterally with the propleural arm.

The **dorsal profurcal lamella** (**dp1l**: Figs 3, 5, 6, 37, 41, 45) extends along the dorsal surface of the profurcal arm. The **longitudinal line of the dorsal profurcal lamella\*** (**ld1l**: Figs 3, 5, 6, 45) divides the dorsal profurcal lamella into a median and a lateral area. The triangular **anterior profurcal lamella\*** (**ap1l**: Figs 3, 5, 6, 39, 40, 44) extends anteriorly along the longitudinal submedian line of the dorsal profurcal lamella, whereas the longitudinal **posterior profurcal lamella** (**pp1l**: Figs 3, 6, 40, 44, 45) extends along the posterior margin of the dorsal profurcal lamella. The **ventral profurcal lamella\*** (**vp1l**: Figs 3, 5, 6, 40, 41, 45) extends along the anteroventral surface of the profurcal arm.

*Muscles.* The **propleuro-postoccipital muscle** originates from the propleuron and has two bands. The **median band** (**pl1-pocm**: Figs 3, 4, 42, 43, 46) originates from the propleural epicoxal sulcus. The **lateral band** (**pl1-pocl**: Figs 3, 42) originates from the anterior part of the lateral propleural area. The tendon of the propleuro-postoccipital muscle extends lateral to the cervical prominence. The **propleuro-procoxal muscle** (**pl1-cx1**: Figs 3, 43) originates anteriorly on the lateral propleural area, posterodorsal of the origin of the lateral band of the propleuro-postoccipital muscle. The **propleuro-protrochanteral muscle** (**pl1-tr1**: Figs 3, 42,

43) originates from the dorsal propleural area. The *profurco-laterocervical muscle* (*fu1-cv*: Figs 4, 5, 39, 44) originates from a tendon arising from the anterior edge of the anterior profurcal lamella and inserts on the cervical apodeme. The rodlike *laterocervico-procoxal muscle* (*cv-cx1*: Fig. 5) originates from the cervical apodeme and inserts on the opposite side from which it arises. The *dorsal profurco-postoccipital muscle* (*fu1-pocd*: Figs 4, 5, 39, 44, 46) originates from the dorsal part of the lateral area of the dorsal profurcal lamella. The *ventral profurco-postoccipital muscle* (*fu1-pocv*: Figs 4, 5, 44, 46) originates partly from the anterior surface of the dorsal profurcal lamella ventral to the site of origin of the dorsal profurco-postoccipital muscle and partly from the median area of the dorsal profurcal lamella. The anterior profurcal lamella separates the dorsal and ventral profurco-postoccipital muscles. The *lateral profurco-procoxal muscle* (*fu1-cx1l*: Figs 5, 37, 46, 57) originates partly from the posterior surface of the dorsal profurcal lamella and partly from the ventral surface of the posterior profurcal lamella. The *medial profurco-procoxal muscle* (*fu1-cx1m*: Figs 5, 46) originates partly from the posteroventral surface of the ventral profurcal lamella and partly from the ventral surface of the profurcal arm laterally. The *prosterno-procoxal muscle* (*ps1-cx1*: Fig. 5) originates partly from the median part of the profurcal arm and partly from the prodiscriminal lamella.

### *Pronotum*

*Skeletal structures.* The pronotum is rigidly attached to the mesothorax. The posteroventral corners of the pronotum extend ventrally and fuse medially behind the procoxae to form a sclerotized ring encircling the propectus. The **anterior rim of the pronotum** (**arp**: Figs 16, 19, 48, 56) is the elevated area along the anterior margin of the pronotum, delimited posteriorly by the **pronotal cervical sulcus\*** (**prcs**: Figs 7, 16, 19, 48, 56, 61, 105). In Teleasinae, the **anterior process of the pronotum\*** (**apr**: Figs 35, 47) is a beaklike projection on the median broadened part of the anterior rim of the pronotum. The longitudinal **epomial carina** (**epc**: Figs 7, 16, 19, 48, 49, 51, 56, 61) extends from the anterior rim of pronotum to the **pronotal suprahumeral sulcus\*** (**pss**: Figs 7, 16, 19, 36, 48, 49, 56, 105) and is usually straight or slightly curved, but bends medially in *Nixonia* (Fig. 51). The epomial carina separates the concave and usually setaceous **cervical pronotal area\*** (**cpa**: Figs 16, 19, 49, 56, 59, 61) and the usually bare **lateral pronotal area\*** (**lpa**: Figs 16, 19, 49, 56, 59, 61). The pronotal suprahumeral sulcus extends along the dorsal margin of the pronotum. The pronotal suprahumeral sulcus delimits the **dorsal pronotal area\*** (**dpa**: Figs 7, 16, 19, 39, 48, 49, 56, 105), which is usually narrow and not visible dorsally. In some scelionids the dorsal pronotal

area is enlarged, triangular, and visible dorsally (Figs 39, 56). In *Archeoteleia*, a **dorsal incision of the pronotum\*** (**dipr**: Figs 48–50) is on the posterior part of the dorsal margin of pronotum. The incision fits with the **anterior extension of the preaxilla\*** (**epax**: Figs 48, 75). The **posterior pronotal inflection** (**ppi**: Figs 8, 48, 50, 52–55, 60, 62) extends along the posterior margin of the pronotum delimiting a narrow posterior area of the pronotum. In *Sparasion*, the posterior area of the pronotum is enlarged, and the posterior pronotal inflection corresponds with the **posterior pronotal sulcus\*** (**pps**: Figs 35, 56, 96). The posterior pronotal sulcus is usually absent from other Scelionidae, but is present dorsally in Teleasinae (Figs 35, 96).

The **mesothoracic spiracle** (**sp2**: Figs 8, 19, 48, 52, 60, 61) is near the posterior margin of the pronotum. The trachea of the mesothoracic spiracle extends through an opening between the dorsal part of the posterior pronotal inflection and the lateral wall of the pronotum (Figs 8, 50, 52). The posterior pronotal inflection merges dorsally with the **dorsal pronotal inflection** (**dpi**: Figs 8, 50, 52–54, 60) and forms the **posterodorsal edge of pronotum\*** (**pdep**: Figs 8, 48, 52–54, 97, 105).

The **netrion** (**net**: Figs 7, 16, 19, 35, 36, 48, 49, 51, 96, 97, 105) is a posteroventral region of the pronotum that is differentiated in sculpture from the lateral pronotal area and is delimited anteriorly by the **netrion sulcus** (**nes**: Figs 7, 16, 49, 51). The netrion sulcus usually is distinct and usually extends to the posterolateral margin of the pronotum ventral to the mesothoracic spiracle; it corresponds internally to the **netrion apodeme** (**nea**: Figs 8, 50, 52, 53, 57, 58, 64, 65). The netrion apodeme originates anteriorly from the anterior margin of the ventral pronotal bridge and usually fuses with the posterior pronotal inflection below the mesothoracic spiracle. The ventral bridge of the pronotum extends between the ventral ends of the netrion on opposite sides of the pronotum.

Both the netrion apodeme and corresponding external structures vary in Scelionidae. In *Scelio* (Figs 57, 58), *Barycous*, *Apegus*, and *Calliscelio* the netrion apodeme is well developed, whereas in *Nixonia* (Fig. 53), *Archaoteleia* (Figs 50, 52), *Gryon*, *Idris*, Telenominae (Fig. 60), Teleasinae (Figs 59, 65), and the netrion apodeme is marked only by a shallow ridge or is reduced. The netrion apodeme and the netrion sulcus is absent from *Sparasion* (Figs 54, 55, 62). In *Nixonia* (Fig. 53), the netrion apodeme extends parallel to the posterior pronotal inflection and the trachea extends between the netrion apodeme and the posterior pronotal inflection.

*Muscles.* The **occluser muscle apodeme** (**oma**: Figs 50, 52, 58, 59) is located anterior to the netrion apodeme. The occluser muscle apodeme is present in *Archaoteleia* (Figs 50,

52), Teleasinae (Fig. 59), *Calliscelio*, *Scelio* (Fig. 58), *Gryon*, *Probaryconus* and *Idris*, but absent from *Nixonia*, *Sparasion* (Figs 53–55), *Trissolcus*, *Telenomus* (Fig. 60), *Baryconus* and *Apegus*. In many Scelionidae, the **pronoto-first thoracic spiracle muscle** (*t1-sp2*: Figs 7, 8, 55, 58) originates from the occlusor muscle apodeme. If the apodeme is absent, then the muscle originates partly from the anterior surface of the netrion apodeme and partly from the lateral wall of the pronotum anterior to the netrion apodeme or the posterior pronotal inflection (Fig. 55). In *Nixonia*, the muscle originates posterior to the netrion apodeme.

The dorsal pronotal area serves as the site of origin of the **pronoto-procoxal** (*t1-cx1*: Figs 7, 8, 57, 63, 65, 98, 116), **pronoto-postoccipital** (*t1-poc*: Figs 7, 8, 42, 55, 98, 116), **pronoto-laterocervical** (*t1-cv*: Figs 7, 8, 42, 57, 116), and the **pronoto-propleural** (*t1-pll*: Figs 4, 7, 8, 42, 55, 57, 116) muscles. The pronoto-procoxal muscle originates from the lateral most part of the dorsal pronotal area and extends to the procoxa. The pronoto-postoccipital muscle originates anterior to the site of origin of the pronoto-procoxal muscle and dorsal of the site of origin of the pronoto-laterocervical muscle. The pronoto-propleural muscle originates anterior of the site of origin of the pronoto-laterocervical muscle and extends lateral to the pronoto-postoccipital muscle and medial of the pronoto-laterocervical muscle. The pronoto-propleural muscle inserts on the **dorsal incision of the propleuron\*** (*dip*: Fig. 4). The **pronoto-profurcal muscle** (*t1-fu1*: Figs 6–8, 39, 57, 116) originates from the lateral pronotal area and inserts on the lateral part of the dorsal margin of the dorsal profurcal lamella.

### *Mesoscutum*

*Skeletal structures.* The vertical, weakly sclerotized **first phragma** (*ph1*: Figs 9, 66, 68–72, 78, 122) extends along the anteroventral margin of the mesoscutum between the **preaxillae** (*pax*: Figs 9, 17, 18, 19, 72, 74–79). It is entirely hidden by the pronotum and is continuous anterodorsally with the well sclerotized **vertical lobe of the mesoscutum\*** (*vrtn*: Figs 9, 69, 70, 72), and is well developed and partly divided ventrally by an incision in *Nixonia* and *Sparasion* (Fig. 68), but is reduced and undivided (Figs 66, 69) in other Scelionidae. The **ventral apodeme of the first phragma\*** (*aph1*: Figs 9, 66, 71, 73) is lateral on the ventral margin of the first phragma. In *Calliscelio*, *Calotelea* and *Anteromorpha* the apodeme is well developed, and its ventral end curves posteriorly (Figs 72, 73). In Teleasinae, Gryonini, *Idris*, *Probaryconus* and Telenominae the apodeme is cup-shaped and on the posterior part of the first phragma (Fig. 71). In *Apegus*, *Baryconus*, and *Scelio* the cup-shaped apodeme is just anterior to the posterior end of the first phragma (Fig. 66). The apodeme is absent from *Nixonia* and *Sparasion*.

The **lateral margin of mesoscutum\*** (**lmms**: Figs 9, 17) fits into the dorsal pronotal inflection. The **mesoscutal suprahumeral sulcus** (**shms**: Figs 9, 16, 17, 19, 72, 75, 83, 84) corresponds externally with the first phragma and the vertical lobe of the mesoscutum. The **mesoscutal humeral sulcus** (**mshs**: Figs 9, 17–19, 72, 75, 83, 84) extends between the posterior end of the mesoscutal suprahumeral sulcus and the posterolateral edge of the mesoscutum.

The **antero-admedian line** (**aal**: Figs 16, 17, 69, 75, 80) originates from the anterior margin of the mesoscutum. The transverse **skaphion carina\*** (**skpc**: Figs 9, 16, 17, 80, 81) delimits the **skaphion** (**sk**: Figs 9, 16, 17, 19, 80, 81) anteriorly on the mesoscutum in some Scelionidae.

The vertical preaxilla is separated from the horizontal part of the mesoscutum by the **parascutal carina** (**psc**: Figs 9, 17, 18, 72, 74–79). The **anterior notal wing process** (**anwp**: Figs 9, 17, 18, 75, 77, 79) is on the ventrolateral part of the preaxilla. The anterior part of the first axillary sclerite articulates with the anterior notal wing process. The preaxilla extends anteriorly to form the anterior extension of the preaxilla in *Archaeotelia* (Figs 48, 75). The anterior extension of the preaxilla fits into the dorsal incision of the pronotum. The preaxilla extends posteriorly to form the **posterior extension of the preaxilla\*** (**pep**: Figs 9, 17, 85, 123). The oblique **preaxillar carina\*** (**pxc**: Figs 9, 17, 18, 76, 78, 79) extends across the preaxilla and separates the articulation for the **tegula** (**tga**: Figs 16, 19, 74, 76, 97;) from the anterior notal wing process. The anterior margin of the tegula fits to the posterodorsal edge of pronotum.

The longitudinal **median mesoscutal line** (**mml**: Figs 17, 18, 82, 83) extends medially for most of the mesoscutum in some Scelionidae, terminating posteriorly in the transscutal articulation. Although the line is well developed in some genera, it never corresponds with an internal carina. The **notaulus** (**not**: Figs 9, 17–19, 75, 80, 82, 83, 84; Gibson 1985) is a submedial longitudinal furrow extending anteriorly from the posterior edge of the mesoscutum. The notaulus may be abbreviated anteriorly. Lateral of the notaulus is the usually indistinct **parapsidal line** (**prsl**: Figs 9, 17, 18, 75, 77, 82, 84). The presence of notauli varies in Scelionidae and in some Teleasinae only males have notauli. Each notaulus usually is marked by a foveolate or simple sulcus (Figs 75, 82), but in some *Sparasion* species it is marked by a row of foveae (Fig. 84) and in a few taxa it is expressed as a distinct ridge (Fig. 83).

*Muscles.* The first phragma serves as the anterior attachment site for the **first phragmo-second phragmal muscle** (**ph1-ph2**: Figs 46, 70, 81, 98, 122). The anterior site of attachment of the muscle extends from the phragma onto the mesonotum and corresponds with the anterior-

admedian line. The skaphion carina posteriorly crosses the anterior attachment site of the first phragmo-second phragmal muscle. The *first phragmo-propleural muscle* (*ph1(t1)-pll*: Figs 9, 66) and *first phragmo-postoccipital muscle* (*ph1(t1)-poc*: Figs 9, 66) originate from the anterior surface of the first phragma. The *pronoto-first phragmal muscle* (*t1-ph1*: Figs 7, 8, 55, 58, 63, 98, 116) originates from the lateral pronotal area and inserts on the anterior surface of the first phragma.

The median mesoscutal line extends along the border between the two bands of the first phragmo-second phragmal muscles. The notauli mark the border between the attachment sites of the first phragmo-second phragmal and *first mesopleuro-mesonotal muscle* (*pl2-t2a*: Figs 70, 98). The posterior part of the site of origin of the first mesopleuro-mesonotal muscle corresponds to the parapsidal line.

### *Scutellar-axillar complex*

*Skeletal structures.* The mesoscutum is separated from the scutellar-axillar complex by the **transscutal articulation** (*tsa*: Figs 9, 17–19, 72, 74, 75, 78, 83, 84, 86, 90). The usually foveolate **scutoscutellar sulcus** (*sss*: Figs 9, 17–19, 72, 74, 75, 78, 83, 84, 86, 90, 95) separates the lateral axilla (Gibson 1985) from the **mesoscutellum** (*scu*: Figs 9, 17–19, 75, 83–88, 90) and usually merges dorsomedially with the transscutal articulation. The scutoscutellar sulcus corresponds internally to the **scutoscutellar ridge** (*ssr*: Figs 85, 87, 89, 91, 92). The oblique **scutellar bridge\*** (*scbr*: Figs 87, 89) originates from the scutoscutellar ridge in Telenominae and Teleasinae and fuses with the posterior part of the mesoscutellum. The scutellar bridge is absent from other Scelionidae. The lateral part of the scutoscutellar sulcus bends anteriorly and extends to the ventral end of the **axillar carina** (*axc*: Figs 9, 17, 18, 76, 77, 79, 88, 90, 91, 93, 95, 96). The axillar carina separates the **dorsal axillar area** (*daa*: Figs 9, 17–19, 76, 77, 79, 88, 90, 93, 95, 96) from the **lateral axillar area** (*laa*: Figs 9, 17, 19, 76, 77, 79, 88, 90, 93, 95, 96). The posterior extension of the preaxilla abuts the anterior part of the **anterior extension of the lateral axillar area\*** (*lapa*: Figs 9, 67, 79, 85, 87, 89, 90, 91–93, 123). The **posterior notal wing process** (*pnwp*: Figs 9, 17, 77, 90, 91, 93) is on the posterior part of the anterior extension of lateral axillar area just behind the posterior extension of the preaxilla. The **transaxillar carina\*** (*tac*: Figs 9, 17–19, 75, 77–79, 88, 95, 96) divides the dorsal axillar area into horizontal and vertical areas. The **axillula** (*axu*: Figs 9, 17–19, 74, 79) is a lateral, vertical area of the mesoscutellum delimited by the **axillular carina** (*auc*: Figs 9, 17–19, 78, 86, 93, 95, 96). In some Scelionidae the axillular carina fuses with the transaxillar carina and forms a longitudinal carina, which delimits the anterolateral, vertical area of scutellar axillar complex

(Figs 95, 96). *Archaeoteleia* lacks an axillular carina (Fig.74) and in *Nixonia* (Fig. 93) it is a weak, reduced carina that arises from the posterolateral margin of the mesoscutellum. In *Archaeoteleia*, *Gryonoides*, and *Neoscelio* the **lateral mesoscutellar spine\*** (**lmsp**: Figs 74, 75, 94, 95) arises laterally from the posterodorsal margin of the axillula. The **postalar process** (**pap**: Figs 9, 17–19, 75, 77, 78, 84, 86–92, 123, 124) arises from the ventral margin of the axilla anteriorly and from the ventral margin of the mesoscutellum posteriorly. In *Xenomerus* and some *Trimorus* the median mesoscutellar spine is located on the posterodorsal part of the mesoscutellum. The **posterior mesoscutellar sulcus\*** (**psu**: Figs 9, 17–19, 84, 86, 88, 90) corresponds internally with the **vertical apodemal lobe of the mesoscutellum\*** (**valm**: Figs 9, 85, 87, 92, 93, 120).

### *Mesopectus*

*Skeletal structures.* The **mesobasalare** (**ba2**: Figs 10, 12, 76, 101) fits into the **anterodorsal incision of the mesopleuron\*** (**adi**: Figs 12, 76, 100).

The oblique **acropoleural sulcus** (**asu**: Figs 19, 76, 94, 96, 97, 100, 105, 107) is on the anterodorsal part of mesopleuron and corresponds internally to the **acropoleural apodeme\*** (**acra**: **Figs 12, 71, 101, 106**) in most Scelionidae. The acropoleural apodeme is absent from *Sparasion* and *Nixonia*. The oblique, externally concave **femoral depression** (**fed**: Figs 19, 74, 94, 96, 97, 99, 100, 105, 107) extends between the speculum (see below) and the posteroventral edge of the mesopleuron. The **pleural pit** (**pp**: Figs 19, 94, 96, 97, 100, 107) on the anterodorsal part of the femoral depression corresponds internally with the **pleural apodeme\*** (**pa**: Figs 10, 12, 64, 65, 67, 101–104, 106, 118). The pleural apodeme is absent from *Nixonia*, and is reduced in *Archaeoteleia* and *Sparasion*. The femoral depression is usually limited anteroventrally by the **mesopleural carina** (**mc**: Figs 19, 36, 94, 96, 97, 99). In some Scelionidae a ventral and a dorsal foveolate sulcus extend alongside the mesopleural carina.

The **acetabulum** (**act**: Figs 10, 11, 16, 35) on the anteroventral part of the mesopleuron accommodates the fore coxa. The **acetabular carina** (**ac**: Figs 10–12, 16, 35, 74, 94, 96, 99, 100, 134) delimits the acetabulum posteriorly. The **postacetabular sulcus\*** (**ats**: Figs 16, 19, 35, 94, 96, 99, 100, 134) extends posteriorly along the acetabular carina. The coriaceous **postacetabular patch\*** (**papc**: Figs 19, 35, 96, 100, 134) is on the lateroventral, convex part of the mesopleuron posterior to the postacetabular sulcus in most Scelionidae. The **sternaulus** (**str**: Figs 16, 19, 96, 134) is an anteriorly curved sulcus extending between the dorsal part of the mesopleural carina and the dorsal end of the postacetabular sulcus. In some cases the sternaulus is well developed and distinctly separated from the foveolate sulcus extending

ventrally to the mesopleural carina (Fig. 96), but usually is less distinct and obscured by other mesopleural structures or by the overall sculpture of the mesopleuron (Figs 36, 94, 97).

The **mesocoxal depression\*** (**mcp**: Figs 10, 99, 134) is the ventral depressed area of the mesothorax that abuts the base of the mesocoxa, in the bottom of which is the mesocoxal cavity. The transverse **ventral mesopleural carina\*** (**vplc**: Figs 10, 12, 16, 19, 96, 99, 100, 134) surrounds the mesocoxal depression. The **mesopleural epicoxal sulcus\*** (**mes**: Figs 16, 19, 96, 99, 100, 134) extends dorsally along the ventral mesopleural carina.

The **posterior mesepimeral inflection** (**mepi**: Figs 11, 12, 106, 108–110, 112–115) extends along the posterior margin of the mesopleuron, curving anteriorly and widened on the dorsal margin of the mesopleuron where it fuses with the impressed dorsal margin of the mesopleuron to form the **posterodorsal edge of the mesopleuron\*** (**pdem**: Figs 10–12, 101, 103, 106, 108–110, 113, 115). The postalar process of the scutellar-axillary complex fits into the impression on the dorsal margin of the mesopleuron. The posterodorsal edge of the mesopleuron extends to the **subalar pit** (**sapi**: Figs 10, 11, 19, 36, 74, 76, 94, 96, 100, 105) and is connected with the mesosubalare. The **mesepimeral ridge** (**meer**: Figs 10–12, 106, 108–115) arises from the mesopleurocoxal condyle and extends along the posterior margin of the mesopleuron anterior to the posterior mesepimeral inflection. Most Scelionidae have a mesepimeral ridge, but is reduced in *Apegus* and *Baryconus* and is absent from *Scelio*. The mesepimeral ridge and the externally corresponding **mesepimeral sulcus\*** (**mees**: Figs 19, 36, 74, 94, 96, 97, 100, 105, 107, 136) delimit the narrow **posterior mesepimeral area\*** (**pmma**: Figs 19, 36, 74, 96, 97, 100). Dorsally, the mesepimeral ridge bends anteriorly and fuses with the posterodorsal edge of mesopleuron. The **dorsal mesopleural inflection** (**dmi**: Figs 10, 94, 103, 108; = mesepimeral inflection *sensu* Ronquist & Nordlander 1989) is anterior to the subalar pit and accommodates the second axillary sclerite (Snodgrass 1942). The **speculum** (**spec**: Figs 19, 36, 74, 94, 96, 97, 100, 105) is the area of the mesopleuron just ventral of the posterodorsal edge of mesopleuron; internally, it corresponds to a concavity. The speculum is limited posteriorly by the mesepimeral ridge and ventrally by the femoral depression. The internal **anterior margin of the speculum\*** (**amsp**: Figs 10, 12, 101, 103, 104, 106, 112) limits the speculum anteriorly. It is a distinct, vertical apodeme that dorsally is fused with the posterodorsal edge of the mesopleuron and externally corresponds to the **prespecular sulcus\*** (**pssu**: Figs 19, 74, 94, 96, 97, 105). The anterior margin of speculum usually diminishes dorsal to the pleural apodeme. In *Telenomus* and *Trissolus* the pleural apodeme fuses with the anterior margin of the speculum, forming an oblique, concave apodeme. In *Psix* and *Paratelenomus* the anterior margin of the speculum is not fused with the pleural apodeme, but extends ventrally to

the mesocoxal articulation (Figs 103, 104) and corresponds externally to the **transpleural sulcus** (**tps**: Figs 19, 105).

A median longitudinal line along the venter of the mesopectus, the meso**discrimen** (**dscr2**: Fig. 134), internally corresponds to the meso**discrimenal lamella** (**dscl2**: Figs 12, 104), which extends between the acetabulum and the **mesofurca** (**fu2**: Figs 11, 12, 46, 108–110, 113). The site of origin of the mesofurca corresponds with the **mesofurcal pit** (**fup2**: Figs 12, 99, 134), which is situated between the mesocoxal depressions. The mesofurca is Y-shaped, with the **lateral mesofurcal arms** (**lmfa**: Figs 10–12, 108–110, 113, 115) connected by the **mesofurcal bridge** (**frb**: Figs 10, 11, 108–110, 113, 116, 117). The **anterior process of the mesofurcal bridge** (**apfb**: Figs 10, 117) is present in *Calliscelio* and *Archaeoteleia*, but not in other Scelionidae. The lateral mesofurcal arm is flattened laterally and extends to the speculum to form the **anterior extension of the mesofurca\*** (**anem**: Figs 10, 12, 108, 112–115). The lateralmost part of the lateral mesofurcal arm is twisted posterodorsally.

*Muscles.* The ventral, convex area of the mesopectus is the ventral site of attachment of the first mesopleuro-mesonotal muscle. The **third mesopleuro-mesonotal muscle** (**pl2-t2c**: Figs 9, 12, 66, 70–72) originates from the ventral apodeme of the first phragma and inserts on the acropleural apodeme of the mesopleuron. The size of the muscle varies depending on how anteriorly the ventral apodeme is located on the first phragma.

The **pronoto-third axillary sclerite of the fore wing muscle** (**t1-3ax2**: Figs 7, 8, 10, 57, 58, 62–65) originates from the netrion in most Scelionidae. The site of origin of the muscle is usually limited anteriorly by the netrion apodeme. In *Sparasion*, the muscle originates from the posterior area of the pronotum that is delimited by the posterior pronotal inflection. The muscle inserts on the 3rd axillary sclerite of the fore wing, sharing a common tendon with the **anterior mesopleuro-third axillary sclerite of the fore wing muscle** (**pl2-3ax2a**: Figs 10, 12, 62, 63, 65, 72, 103, 104, 112). The **posterior mesopleuro-third axillary sclerite of the fore wing muscle** (**pl2-3ax2p**: Figs 10, 12, 62–65, 67, 72, 103, 104, 112, 118) originates dorsal to the site of origin of the **mesopleuro-mesobasalare muscle** (**pl2-ba2**: Figs 10, 12, 67, 103, 104, 118). The anterior mesopleuro-third axillary sclerite of the fore wing muscle originates dorsal to the origin of the posterior mesopleuro-third axillary sclerite of the fore wing muscle.

The number and the sites of origin of muscles inserting on the mesobasalare vary in Scelionidae. All Scelionidae have an **intersegmental membrane-mesobasalare muscle** (**ism1,2-ba2**: Figs 10, 12, 64, 67, 103, 118). In *Scelio*, *Telenomus*, *Trissolcus*, *Gryon*, *Teleasinae*, *Calliscelio* and *Probaryconus* the mesopleuro-mesobasalare muscle originates just anteroventral of the origin of the mesopleuro-third axillary sclerite of the fore wing muscles

and corresponds externally to the sternaulus. *Archaeoteleia* and *Idris* lack the mesopleuro-mesobasalare. In these two genera the ***pronoto-mesobasalare muscle*** (*t1-ba2*: Fig. 7) originates from the ventral bridge of the pronotum medial to the site of origin of the pronoto-third axillary sclerite of the fore wing muscle.

The ***mesopleuro-third axillary sclerite of the hind wing muscle*** (*pl2-3ax3*: Figs 11, 104, 109, 110, 113–116) originates at least partly from the mesopectus. In most Scelionidae, it originates from the posterior surface of the mesepimeral ridge, but in *Scelio*, *Apegus*, and *Baryconus* where the mesepimeral ridge is absent or reduced, the muscle originates from the mesopectus posteroventral to the site of origin of the mesopleuro-mesofurcal muscle (Figs 67, 109, 115). In *Sparasion*, *Nixonia*, and *Scelio* the site of origin of the muscle is shared between the meso- and metapleuron..

In most Scelionidae the ***second mesopleuro-mesonotal muscle*** (*pl2-t2b*: Figs 9, 10, 12, 62–65, 67, 102, 118, 119) is rod-like, originating from the dorsal surface of the pleural apodeme and inserting on the ventral surface of the lateral axillar area. In *Archaeoteleia*, *Nixonia*, and *Sparasion*, where the pleural apodeme is absent, the muscle is fan-shaped and originates from the dorsal part of femoral depression. The ***mesopleuro-mesocoxal muscle*** (*pl2-cx2*: Figs 10, 12, 62–65, 67, 102–104, 112, 118) originates from the dorsal part of the femoral depression just ventral to the site of origin of the second mesopleuro-mesonotal muscle, at least partly from the ventral surface of the pleural apodeme if present. In *Telenomus* and *Trissolcus* the second mesopleuro-mesonotal muscle originates from the dorsal surface of the fused pleural pit apodeme and the anterior margin of the speculum, and the mesopleuro-mesocoxal muscle originates from the ventral part of this structure (Fig. 102).

The ***mesocoxo-mesosubalare muscle*** (*cx2-sa2*: Figs 11, 64, 67, 109–111, 113), originates from the mesocoxa and extends posterior to the mesopleuro-mesofurcal muscle to the subalare. The ***mesosterno-procoxal muscle*** (*s2-cx1*: Fig. 10) originates from the anterior part of the mesodiscriminal lamella.

The ***mesopleuro-mesofurcal muscle*** (*pl2-fu2*: Figs 10, 12, 108, 111, 112, 114) originates from the anterior surface of the mesepimeral ridge and inserts on the external surface of the flattened, membranous anterior extension of the mesofurca. The site of origin extends anterior of the mesepimeral ridge dorsally and covers the internal surface of the speculum. The ***lateral mesofurco-mesotrochanteral muscle*** (*fu2-tr2l*: Figs 10–12, 67, 109, 111, 112, 114, 115, 118, 119) originates from the internal part of the mesofurca. In *Nixonia*, *Sparasion*, *Gryon*, *Idris*, and *Archaeoteleia* the ***median mesofurco-mesotrochanteral muscle*** (*fu2-tr2m*: Figs 10, 11, 111) originates from the ventral surface of the lateral mesofurcal arm medial to the site of

origin of the lateral mesofurco-mesotrochanteral muscle. The *mesofurco-mesocoxal muscle* (*fu2-cx2*: Figs 10, 11, 46, 109, 110, 113) originates partly from the lateral mesofurcal arms and partly from the base of the mesofurca. The *mesosterno-mesocoxal muscle* (*s2-cx2*: Figs 10, 46, 104) originates partly from the base of the mesofurca and partly from the posterior part of the mesodiscriminal lamella. The slender, rodlike *dorsal mesofurco-profurcal muscle* (*fu2-fu1d*: Figs 10–12, 46, 116) originates from the lateral part of the lateral mesofurcal arm and inserts on the posterior surface of the posterior profurcal lamella. The fan-shaped *ventral mesofurco-profurcal muscle* (*fu2-fu1v*: Figs 10–12, 46, 116, 117) originates from the mesofurcal bridge and inserts on the base of the profurca. In *Calliscelio* and *Archeoteleia* the muscle originates partly from the anterior process of the mesofurcal bridge. The *prosterno-procoxal muscle* (*ps1-cx1*: Fig. 5) originates partially from the mesodiscriminal lamella.

#### *Mesopostnotum and the second phragma*

*Skeletal structures.* The mesopostnotum is concealed by the mesonotum and the metanotum. The sclerotized, transverse, **ventral mesopostnotal flange** (*vpnr*: Fig. 125) and **dorsal mesopostnotal flange** (*dpnr*: Fig. 125) extend across the mesopostnotum and unite laterally where they are continuous with the anteriorly oriented, well-sclerotized **mesolaterophragma** (*lph2*: Figs 118–120, 122). The mesopostnotum is connected to the mesoscutum via the dorsal mesopostnotal flange and to the metanotum via the ventral mesopostnotal flange, and is membranous between the two flanges. The **dorsal mesopostnotal incision\*** (*dmpi*: Figs 120, 125) is situated medially on the dorsal margin of the mesopostnotum. The laterophragma is connected anteriorly with the mesosubalare and laterally with the **humeral sclerite of the metanotum** (*hmsc*: Figs 89, 121, 123–125, 142, 144). The **axillary lever** (*pnap*: Figs 87, 89, 118, 119, 120–123, 125) is located medial to the humeral sclerite. The **second phragma** (*ph2*: Figs 78, 87, 89, 120–122, 125, 142) arises ventrally from the mesopostnotum. The pseudophragma (Ronquist & Nordlander 1989) is absent from all Scelionidae.

*Muscles.* The *mesoscutello-metanotal muscle* (*t2-t3*: Figs 9, 81, 87, 89, 92, 120, 125) originates posteriorly from the scutoscutellar ridge and extends dorsally of the dorsal mesopostnotal incision. The *mesofurco-laterophragmal muscle* (*fu2-ph2*: Figs 10–12, 109–111, 115, 121) originates from the dorsal surface of the lateral mesofurcal arm just lateral to the origin of the dorsal mesofurco-profurcal muscle and inserts on the mesopostnotal apodeme. The first phragmo-second phragmal muscle is attached to the anterior surface of the second phragma.

### *Metanotum*

*Skeletal structures.* The **transmetanotal carina** (**tmc**: Figs 17–19, 86, 88, 97, 98, 126, 130, 131, 136, 137) delimits the smooth, concave **supraalar area** (**saa**: Figs 18, 19, 130, 131) anterolaterally on the metanotum. The anterior notal wing process is on the humeral sclerite of the metanotum and the posterior notal wing process is on the anterior part of the supraalar area. The usually foveolate transverse **metanotal trough** (**mnt**: Figs 17–19, 98, 105, 130, 131, 136, 137) medially and anteriorly delimits the elevated **metascutellum** (**msct**: Figs 17–19, 98, 105, 131, 133, 137). Laterally, the trough curves posteriorly to extend along the posterior margin of the metanotum. The metascutellum may be limited laterally by the **metascutellar carina\*** (**mts**: Figs 17, 86, 88, 98, 131, 133). The metascutellum is often furnished with one or more **metanotal spines\*** (**mns**: Figs 17, 18, 88, 97, 98). These usually originate from the middle of the metascutellum or from the metascutellar carina.

Internally, the metanotal trough corresponds to the **internal metanotal ridge\*** (**mnt**: Figs 126, 127, 132, 142, 144). The metanotal ridge bifurcates medially to surround the **internal chamber of the metanotum\*** (**chm**: Figs 126, 144, 151), which corresponds to the metascutellum. The **muscle-bearing process of the metanotum** (**mbpm**: Figs 124, 126, 132, 142, 144, 151) is located ventrally on the anterior part of the metanotum.

*Muscles.* The mesoscutello-metanotal muscle inserts on the dorsal margin of the metanotum above the chamber of the metanotum. The **metapleuro-metanotal muscles** (**pl3-t3a, b**: Figs 14, 15, 132, 144, 151, 152) insert on the muscle-bearing process of the metanotum. The **metanoto-metatrochanteral muscle** (**t3-tr3**: Figs 13, 15, 67, 143, 145, 146, 151) originates from the humeral sclerite of the metanotum.

### *Metapectal-propodeal complex*

*Skeletal structures.* The metapectus is delimited dorsally from the propodeum by the **metapleural carina** (**mtpc**: Figs 18, 19, 129, 131, 133–140), which extends from just ventral of the **metapleural arm** (**mtam**: Figs 13, 18, 19, 129, 131, 139, 141, 143, 146, 152) to the metacoxal articulation, passing anteroventral to the **propodeal spiracle** (**T1sp**: Figs 15, 18, 19, 129, 133, 135–137, 139). The metapleural arm is the anterodorsal extension of the metapleuron and is delimited from it by the anteriormost extension of the propodeum (prespiracular area, see below).

The metapleuron is divided by the sigmoid **metapleural sulcus** (**mtps**: Figs 18, 19, 96, 129, 131, 133, 134, 136–140) into the **dorsal** and **ventral metapleural areas\*** (**dmpa**, **vmpa**:

Figs 18, 19, 96, 129, 131, 138). It is usually complete and extends from the metapleural arm to the posterior part of the metacoxal articulation some distance ventral to the metapleural carina; internally it corresponds to the **metapleural ridge** (**mprg**: Figs 13–15, 132, 144, 149, 152). The **metapleural apodeme** (**mpa**: Figs 13, 15, 132, 141–144, 148, 150, 152) is on the metapleural ridge and corresponds externally to the **metapleural pit** **\*(metp**: Figs 18, 19, 96, 131, 133, 139, 140). In some taxa the metapleural ridge is reduced or absent, in which case only the metapleural apodeme is present (Fig. 142).

The **paracoxal sulcus** (**pcxs**: Figs 19, 99, 105, 131, 133, 138, 140) originates dorsally from the metapleural sulcus and extends ventrally along the anterior margin of the metapleuron; internally it corresponds to the **paracoxal ridge** (**pcxr**: Figs 13–15, 67, 132, 141–146, 151). In *Sparasion* and *Archaeoteleia* (Figs 141–144) the paracoxal ridge is continuous with the dorsal, vertical part of the metapleural ridge; in other Scelionidae it diminishes ventral to the metapleural ridge (Figs 142, 143, 145, 146). The posteroventrally extended **metapleural epicoxal sulcus\*** (**meps**: Figs 18, 19, 131, 134) and **metapleural epicoxal carina\*** (**mpxc**: Figs 18, 19, 94, 96, 99, 134, 140) originate medially from the paracoxal sulcus and delimit the **metapleural triangle** (**mtp**: Figs 19, 96).

The paired **metepisternal depression** (**mtad**: Figs 13, 99, 134, 142–144, 151) is on the anteroventral margin of the metepisternum. The **ventral carina of the metapleuron\*** (**vcmp**: Figs 13, 14, 18, 99, 134, 142–144) separates the metepisternal depression from the **metacoxal depression\*** (**mcxd**: Figs 18, 99, 134, 137, 138, 140). The metacoxal foramen is situated in the middle of the metacoxal depression, which accommodates the base of the metacoxa.

The **metafurcal pit** (**fup3**: Figs 18, 129, 134) is between the metacoxal foramina; internally it corresponds to the base of the **metafurca** (**fu3**: Figs 14, 15). The metafurca is Y-shaped, its base situated anteriorly on the **metadiscriminal lamella** (**dscl3**: Figs 14, 104, 145, 147), which extends between the metafurcal pit and the paracoxal ridge. In some Scelionidae the **metadiscrimen** (**dscr3**: Figs 99, 134) is marked by a row of punctures (Fig. 99). In Telenominae, Gryonini, and Baeini the paracoxal ridge does not extend posterior to the lateral metafurcal arms and the metadiscriminal lamella is square in lateral view (Figs 14a, 142, 145). In other Scelionidae the metafurca is slanted anteriorly and the paracoxal ridge extends medially to the metafurcal arms, in which case the metadiscriminal lamella is triangular in lateral view (Figs 14b, 141, 143, 144). The **metafurcal arm** (**mtfa**: Figs 13–15, 132, 141–144) is bent posteriorly before fusing with the metapleural apodeme. The site of fusion is distinct. The **dorsal** and the **ventral metafurcal lamellae\*** (**dmfl**, **vmfl**: Figs 13, 132, 141, 142; =114, 115 *sensu* Ronquist & Nordlander 1989) extend along the metafurcal arm.

The posterior thoracic spiracle (Vilhelmsen 2000a) is apparently absent from Scelionidae. The propodeal spiracle delimits the posterior margin of the narrow, triangular **prespiracular propodeal area\*** (**pspp**: Figs 18, 19, 133, 135–137, 139, 140), which separates the metapleural arm from the rest of the metapleuron. The **third phragma (ph3**: Figs 13, 15, 128, 132, 141, 143–146, 151, 152) is a low transverse carina that extends along the anterior margin of the propodeum and diminishes medially. The **dorsal propodeal inflection\*** (**dpin**: Figs 15, 128) extends along the dorsal margin of the propodeum posterior to the third phragma. The **metapleural wing articulation (plwa3**: Figs 15, 124, 128, 141, 146) is on the anterior end of the dorsal propodeal inflection just posterior to the metapleural arm. The usually oblique **lateral propodeal carina (lpc**: Figs 15, 18, 19, 129, 131, 133, 135–140) crosses the posterior part of the propodeum and separates the **lateral propodeal area (lpar**: Figs 18, 129, 131, 133, 135–137, 140) from the **metasomal depression (metd**: Figs 18, 129, 131, 133, 135, 137, 138, 140). The shape, expression, and location of the lateral propodeal carina vary and in some Scelionidae the anterodorsal end of the carina extends over the dorsal margin of the propodeum to form a projection (e.g., *Probaryconus*). The shape and dorsal extension of the metasomal depression correlate with structures on the petiole. In those females having the ovipositor housed within the dorsal protuberance of the metasoma (Austin and Field 1997), the metasomal depression is also extended to receive the enlarged site of attachment of the petiole. The dorsal ends of lateral propodeal carinae are far from each other in these cases (Fig. 137), whereas the carinae almost fuse dorsally if the petiole is simple. The dorsal margin of the metasomal depression is simple in most Scelionidae, but in *Nixonia* the dorsal margin is projected into a median spine (Fig. 138, 139). Some Scelionidae have the lateral propodeal carina fused with the metapleural carina (Figs 129, 131). Usually, the lateral propodeal carina is fused with one of the posteriorly oriented oblique carinae that originate from the anterodorsal margin of the propodeum medial to the propodeal spiracle. The number and topology of these posteriorly oriented dorsal carinae vary. The **plica (plc**: Figs 18, 19, 136, 140) is a carina that originates just medial of the propodeal spiracle. The plica fuses with the lateral propodeal carina to form the **posterior propodeal projection\*** (**ppp**: Figs 18, 19, 136, 140). The plica separates the usually setaceous **plical area (pla**: Figs 18, 136, 140) from the lateral propodeal area. The **propodeal tooth (prth**: Figs 18, 129, 137, 138) is a distinct projection on the lateral margin of the **propodeal foramen (prfo**: Figs 13, 18, 129, 137, 138). The projection serves as the site of attachment of the **anterolateral depression of the petiole\*** (**ldpp**: Figs 153, 155) of the metasoma. The propodeal foramen is encircled by the metasomal depression, which is the posterior, depressed area of the propodeum that accommodates the base of the metasoma. The

metasomal depression is limited dorsolaterally by the lateral propodeal carina and ventrolaterally by the ventral part of the metapleural carina. The metasomal depression sometimes is continuous with the metacoxal depression (Figs 129, 138), but in most Teleasinae, Telenominae, *Gryonini*, *Baeini*, where the propodeal foramen is situated more dorsally, it is separated from the metacoxal depression by the **ventral propodeal carina\*** (**vprc**: Figs 18, 134, 137, 140).

*Muscles.* The **metapleuro-metabasalar muscle** (**pl3-ba3**: Figs 14, 15, 67) originates from the anterior surface of the ventral part of the paracoxal ridge. The **metapleuro-third axillary sclerite of the hind wing muscle** (**pl3-3ax3**: Figs 14, 104, 143, 144, 151, 152) originates from the anterior surface of the metapleural ridge (Fig. 144) or, if the ridge is reduced, from the anterodorsal part of the metapleuron ventral to the metapleural arm (Figs 134, 151, 152). The metapleuro-metanotal (**pl3-t3a, b**: Figs 14, 15, 132, 144, 151, 152) and the **metapleuro-metasubalar muscles** (**pl3-sa3**: Figs 14, 147, 149, 150) originate from the dorsal surface of the metapleural ridge. The metapleuro-metanotal muscle sometimes originates as two separated muscle bands from the metapleuron and insert with a common tendon to the muscle-bearing process of the metanotum. The **metacoxo-metasubalar muscle** (**cx3-sa3**: Figs 14, 150, 152) originates from the lateral margin of the metacoxa, extends posterior to the metapleural ridge, and shares a common tendon with the metapleuro-metasubalar muscle. The **median metapleuro-metacoxal muscle** (**pl3-cx3m**: Figs 14, 15, 145–147, 149) originates from the metadiscal lamella. The **lateral metapleuro-metacoxal muscle** (**pl3-cx3l**: Figs 13–15, 67, 149, 152) originates from the posterior surface of the paracoxal ridge, from the ventral surface of the metapleural ridge, and from the metapleuron below the ridge. The posterior margin of the site of origin of the muscle usually corresponds externally to the ventral part of the metapleural carina. The **metapleuro-metatrochanteral muscle** (**pl3-tr3**: Fig. 13) originates anterodorsal to the origin of the lateral metapleuro-metacoxal muscle. The metanoto-metatrochanteral muscles extend anterior to the metafurcal arm and the metapleural ridge just posterior to the paracoxal ridge. The **metafurco-metatrochanteral muscle** (**fu3-tr3**: Figs 13, 15, 67, 148, 149) originates from the lateral part of the metafurcal arm and shares a common tendon with the metanoto-metatrochanteral muscle. The **metafurco-metacoxal muscle** (**fu3-cx3**: Figs 13, 15, 67, 148, 151) originates from the posterior surface of the ventral metafurcal lamella medial to the metafurco-metatrochanteral muscle. The **metafurco-mesofurcal muscle** (**fu3-fu2**: Figs 10, 15) originates from the anterior surface of the lateral part of the metafurcal arm and inserts on the posterior surface of the lateral mesofurcal arms. The **metafurco-second abdominal sternal muscle** (**fu3-S2**: Figs 13–15, 104, 145–147, 151, 153–155) originates from

the posterior surface of the dorsal metafurcal lamella. In *Sparasion*, the muscle consists of two bands that insert with a common tendon on to the second metasomal sternum. The obliquely oriented **third phragmo-second phragmal muscle** (**ph3-ph2**: Fig. 13) originates from the dorsal surface of the third phragma and inserts on the posterior surface of the second phragma. The **third phragmo-second abdominal tergal muscle** (**ph3-T2**: Figs 13, 14, 67, 143, 145–147, 149, 151–155) originates from the ventral surface of the third phragma and inserts on the dorsal surface of the second abdominal tergite. The anterior margin of the site of origin of the **propodeo-second abdominal tergal muscle** (**T1-T2**: Figs 13, 14, 104, 145, 152–155) corresponds externally to the metapleural carina in most Scelionidae. The **propodeo-second abdominal sternal muscle** (**T1-S2**: Figs 13, 152–155) originates ventral to the site of origin of the propodeal-second abdominal tergal muscle. In *Scelio*, the anterior margin of the origin of the muscle extends anterior of the metapleural carina. The muscle inserts on the border between the second abdominal sternite and tergite. The **propodeo-first metasomal spiracle muscle** (**T1-T1sp**: Figs 13, 14) originates from the posteroventral part of the metapleuron just dorsal to the posterior end of the metapleural ridge. In *Archaeotelia*, *Nixonia*, and *Sparasion* the muscle originates from the **dilator muscle apodeme\*** (**dma**: Fig. 132), which corresponds to the **posteroventral metapleural pit\*** (**pvpp**: Figs 131, 139).

## Discussion

### *Possible exocrine glands*

Scelionidae have numerous coriaceous and usually setaceous patches on the body surface. The correlation between some metasomal coriaceous patches, such as the felt fields, and exocrine glands was discussed by Masner & Huggert (1989) for Platygastriidae and by Mikó & Masner (*in press*) in Scelionidae. These patches usually have a median porelike structure. The coriaceous microsculpture and associated setae may act as an evaporating surface for the release of glandar products (Noirot & Quennedy 1974, Buckingham & Sharkey 1988, Quicke & Falco 1998), and the median pore could serve as an opening of class III gland cells (Noirot and Quennedy 1974). Many Scelionidae have some coriaceous patches with median porelike openings on the head and mesosoma similar to that found on the metasoma (Fig. 30), *viz.*, the frontal, genal, vertex, and postacetabular patches. These patches are distinct only in taxa with a smooth body surface, but their relative location is constant. In most Scelionidae, however, the areas where the patches are located are strongly sculptured, and therefore it is impossible to detect them externally.

Some of the coriaceous areas on the body surface could correspond to sites of muscle

attachment, perhaps serving as enlarged surfaces for muscle attachments. This is seen, for example, in the lateral patches on the metasomal terga (Mikó & Masner, *in press*). We assume that the coriaceous orbital band on the head of Telenominae corresponds with the site of origin of either an anterior extension of the mandibular muscles or the cranio-antennal muscle. To differentiate "gland" patches from "muscle" patches externally requires observation of the presence or absence of median porelike openings, and histological examinations are needed to ascertain the nature of the coriaceous areas on the body surface.

The anterior process of the pronotum (Figs 35, 47) in Teleasinae may also be a cuticular modification around the opening of an exocrine gland. This hypothesis is based on the presence of coriaceous sculpture on the anterior rim of the pronotum below the process, perhaps for better evaporation of gland products, and the lack of any corresponding muscle attachment.

Detailed histological examination of coriaceous and setaceous patches may be a fruitful area for further research because the presence, absence, and structure of exocrine glands and their corresponding external features are important for phylogenetic reconstructions and for better understanding of the biology of Hymenoptera (Billen 1990, Billen & Morgan 1998, Isidoro *et al.* 1996, Buckingham and Sharkey 1988, Smith *et al.* 2001).

### *Head*

All of the extrinsic muscles of the antenna originate from the tentorium in Hymenoptera (Alam 1951, Dhillon 1966, Duncan 1939, Snodgrass 1942, Ronquist & Nordlander 1989, Vilhelmsen 1996). In Scelionidae, one extrinsic muscle of the antenna, the cranio-antennal muscle, originates from the frons. Both the precise site of insertion and the function of this muscle are unknown, but it may be homologous with one of the extrinsic muscles originating from the tentorium in other Hymenoptera. The origin of the muscle may have shifted to the frons due to the extreme low anterior site of origin of the tentorium, but regardless the presence of the cranio-antennal muscle could be an apomorphy for Scelionidae.

In *Archaeoteleia*, the anterior cranio-mandibular muscle originates from the internal surface of the gena, similar to the situation in *Apis* (Snodgrass, 1942) and our own observations of several hymenopteran groups: *Evania*, *Gasteruption*, *Helorus*, *Proctotrupidae*, *Megaspilus*, *Galesus*, and *Cotesia*. The anterior margin of the origin of the anterior cranio-mandibular muscle does not extend beyond the internal shallow ridge corresponding to the malar sulcus in *Archaeoteleia* or these other hymenopterans. In Scelionidae other than *Archaeotelia*, the border between the anterior cranio-mandibular and cranio-antennal muscles is anterior to the malar ridge, which we consider as a secondary modification in Scelionidae.

Masner (1976, 1980) considered malar striation to be an important character for the generic classification of Scelionidae. It seems probable that a less extensive or totally reduced malar striation correlates with less extended origins of the anterior cranio-mandibular and lateral antennal muscles.

In most Scelionidae the pleurostomal fossa, which serves as the posterior mandibular articulation, is on the posterior margin of the oral foramen. The axis of rotation of the mandible extends between the pleurostomal fossa and the anterior pleurostomal condyle, resulting in a transverse biting motion (Fig. 156). In contrast, *Sparasion* and *Tyrannoscelio* have the pleurostomal fossa located more anteriorly, on the lateral margin of the oral foramen. This, together with the more deeply impressed pleurostomal condyle, effectively shifts the axis of rotation so that the mandibles move in a nearly dorsoventral plane (Fig. 157). The movement of the mandible in *Sparasion* is complemented by the unique location of the abductor muscle of the mandible (*cr-md*). Furthermore, the anterior cranio-mandibular muscle originates from the lateral wall of the head in most Scelionidae, but on the lateral part of the frons in *Sparasion*. The presence of the frontal ledge in *Sparasion* may be developed for strengthening the frons against the stresses caused by the displaced anterior cranio-mandibular muscle.

Scelionidae are highly variable in development of the frontal depression, interantennal process, and associated features. This may, in part, correspond with the development of the cranio-pharyngeal plate muscle. In *Baryconus* the frontal depression is often very deep and its margins carinate (the submedian carinae) and the origin of the cranio-pharyngeal plate muscle is also the most extended. However, the frontal depression receives the antennal scape when it is depressed to the head and therefore may be considered to be functionally homologous with the scrobal depression of some Chalcidoidea (Gibson 1997). Most of the genera generally considered plesiomorphic for the family, such as *Nixonia*, *Plaumannion*, *Huddlestonium*, and *Archaeoscelio*, have an impression on the gena below the eye into which the scape fits.

Different patterns of sclerotization between the occipital and oral foramina were discussed by Vilhelmsen (1999). He assumed that the sclerotization was formed by a hypostomal bridge in the common ancestor of the Cephoidea, Siricoidea, Orussidae and Apocrita. The hypostomal bridge is formed by the fusion of the hypostomae medially, as indicated by continuity of the hypostomae between the maxillary condyles. In *Orussus* and many Apocrita, however, the hypostomal bridge is largely replaced by a postgenal bridge formed by the medially expanded postgenae. In some Apocrita and in *Orussus* a single median sulcus is present on the postgenal bridge. Microtrichia are found on the lateral margin of this sulcus suggesting that it has been formed by the invagination of the dorsal part of the

hypostomal bridge.

The condition in Scelionidae resembles that of *Orussus*, in which the median sulcus of the postgenal bridge is margined with microtrichia (Fig. 31). In these cases the hypostomal sulcus is interrupted medially. We consider therefore the sclerotized area between the oral and occipital foramina as postgenal in origin, and therefore prefer to use the term postgenal pit instead of hypostomal pit for the pit located on the postgenal bridge. In Teleasinae, however, the median sulcus of the postgenal bridge is absent (Figs 30, 32) similar to the condition in *Xiphydria* (Xiphydriidae) and those apocritans where the hypostomal bridge is most distinct. In these taxa the hypostomal bridge is covered with minute microtrichia and is limited laterally from the postgenae by a pair of sulci. The sulci correspond internally to ridges continuous with the tentorium. The hypostomal sulcus is continuous with the sulci laterally delimiting the hypostomal bridge. Although the sclerotized area between the occipital and oral foramina is delimited by a pair of sulci similar to those in *Xiphydria*, these do not correspond to any internal ridges. Moreover, the postgenal pits, which mark the posterior site of origin of the tentorium, usually are located medial of these sulci, and the hypostomal sulcus in Teleasinae is continuous medially. There are similar sulci delimiting a median area of the postgenal bridge in other Scelionidae having a well-developed median sulcus of the postgenal bridge. On the basis of these observations we conclude, that the sclerotized area between the occipital and oral foramina of Teleasinae is indeed the postgenal bridge, and the median sulcus of the postgenal bridge is secondarily reduced.

Masner (1979a, 1983) and Mineo & Villa (1982) described numerous carinae on the posterior surface of the head in Gryonini that are useful for species differentiation and species-group characterizations. Most of these carinae cross or limit the attachment sites of different bands of the posterior cranio-mandibular muscle. Therefore, they probably serve to reinforce the posterior wall of the head, stabilizing it against stresses caused by contractions of these muscles. Of the terminology proposed, we are reluctant to accept the term hypostomal sulcus *sensu* Masner (1983), which delimits a triangular, impressed area for the propleura. In Hymenoptera, the hypostomal sulcus dorsally delimits the oral foramen (Chapman 2004, Vilhelmsen 1999). We also reject the term postoccipital sulcus proposed by Mineo & Villa (1982) for the same structure, because the sulci are outside the postocciput. Rather, we suggest the term postgenal sulcus in preference to the terms proposed by Masner, Mineo, and Villa.

The internal apodeme corresponding with the preocellar pit is connected to the brain via an epidermal cell bundle and may act as suspension to support the brain (Isidoro and Bin 1994).

The distance between the postgenal pits and the posterior tentorial pits is correlated with the length of the incorporated part of the anterior tentorial arm (ventral lamella of the tentorium). Usually, the shorter the head the longer the incorporated part and therefore the longer the distance between the posterior and hypostomal tentorial pits.

In Hymenoptera, the anterior tentorial pit generally corresponds with the attachment site of the anterior tentorial arm and is distinctly separated from the pleurostomal condyle (Snodgrass 1942, Ronquist & Nordlander 1989, Gibson 1997, Huber and Sharkey 1993). In these taxa, the clypeus is delimited dorsally by the epistomal sulcus, represented internally by the epistomal ridge, and laterally by the clypeo-pleurostomal line. The anterior tentorial arm originates from the anterior margin of the oral foramen in most Scelionidae, and the inverted U-shaped epistomal ridge extends completely to the oral foramen. Therefore, in Scelionidae the clypeus is delimited only by the epistomal sulcus, and the clypeo-pleurostomal sulcus is absent.

### *Propectus*

The propleural arm is well developed in most Hymenoptera, serving as the site of origin of muscles inserting on the protrochanter, mesofurca and pronotum. Two muscle bands insert on the protrochanter in most Apocrita, one originating from the propleural arm and the other from the propleuron (Duncan 1939, Snodgrass 1942, Vilhelmsen 2000b). The mesofurco-propleural arm muscle originates partly from the propleural arm and partly from the "adjacent crest" of the profurcal arm in *Vespula* (Duncan 1939). The propleural arm is reduced in Scelionidae; thus, the sites of origin of the above muscles have been transferred to other propectal areas. The profurco-pronotal muscle of Scelionidae may be homologous with the propleural arm-pronotal muscle of other Hymenoptera because of the relative position of the pronotal site of attachment of the muscle and because the muscle appears to cross over the reduced propleural arm. In Scelionidae, the depressor of the protrochanter originates exclusively from the propleuron. The dorsal mesofurcal retractor of the propectus inserts exclusively on the posterior profurcal lamella in Scelionidae, which may be homologous with the "adjacent crest" of the profurcal arm (Duncan 1939).

The profurcal bridge is absent from Scelionidae, *Vespula* (Duncan 1939), Mymarommatoidea (Vilhelmsen and Krogmann 2006 and most Chalcidoidea (Krogmann and Vilhelmsen 2006) but is present in *Ibalia* (Ronquist & Nordlander 1989), *Apis* (Snodgrass 1942), *Megalyra*, and *Orthogonalys* (Vilhelmsen 2000b).

There is only one profurcal pit in basal Hymenoptera and some Apocrita (Ronquist & Nordlander 1989, Duncan 1939, Snodgrass 1942), but there are two well separated furcal pits

in Scelionidae, similar to that reported in *Stenobracon* (Alam 1951) *Apis* (Snodgrass 1942) and most Chalcidoidea (Krogmann & Vilhelmsen 2006)..

### *Pronotum*

In *Nixonia*, the netrion sulcus extends anterior to the mesothoracic spiracle (Masner 1979: fig. 1, Gibson 1985), whereas in other scelionids it extends to the posterolateral margin of pronotum below the mesothoracic spiracle (Masner 1979: e.g., figs 4–8). Consequently, the mesothoracic spiracle is on the netrion in *Nixonia*, and in other scelionids it is located on the posterodorsal edge of the pronotum, distinctly above the netrion (Gibson 1985). Because of the different position relative to the trachea, the netrion apodeme in *Nixonia* may be only functionally homologous with that of other scelionids.

Masner (1979) suggested that the netrion apodeme might serve for muscle attachment. Gibson (1985) reported that the netrion apodeme lacked muscle attachment and concluded that its main function is to strengthen the lateroventral part of the pronotum, possibly related to the ringlike structure of the pronotum. In Scelionidae, the pronoto-third axillary sclerite of the fore wing muscle originates partly from the netrion (Figs. 7, 8: t1-3ax2) as a pronotal flexor of the fore wing, and the netrion apodeme forms the anterior limit of the muscle's attachment site in most species. The same muscle originates entirely from the mesopectus in other hymenopterans, including the closely related Platygasteridae. The only taxon other than Scelionidae having a pronotal origin of the flexor of the fore wing is Vanhorniidae. *Sparasion* lacks a netrion apodeme, but the posterior pronotal inflection is located more anteriorly to delimit a narrow posterior area on the pronotum. The pronotal flexor of the fore wing originates from this area; therefore, we consider this area to be functionally equivalent with the netrion, and the posterior pronotal inflection as functionally equivalent with the netrion apodeme.

Gibson (1985) proposed that the posterior pronotal inflection is the reduced prepectus that has fused to the posterior margin of the pronotum. He justified this hypothesis based mainly on the location of occlusor muscle apodeme, which is on the prepectus when this is independent, but on or anterior to the posterior pronotal inflection in almost all Scelionidae. Although, in some scelionid genera the occlusor of the first spiracle originates from the occlusor muscle apodeme anterior to the netrion as reported by Gibson 1984, most lack the occlusor muscle apodeme and the muscle originates from the anterior surface of the netrion apodeme or from the lateral pronotal area anterior to the netrion apodeme. Following Gibson (1985), the presence of the occlusor muscle apodeme is plesiomorphic and its absence in Scelionidae is the result of secondary loss. The reduction of the occlusor muscle apodeme

may be related with the development of the netrion apodeme. The posterior position of the occlusor muscle in relation to the netrion apodeme in *Nixonia* is consistent with the suggestion that the netrion apodeme of *Nixonia* may not be homologous with that of other Scelionidae.

Snodgrass (1942) and Alam (1951) reported the presence of a prophragmo-laterocervical muscle in Apocrita. Vilhelmsen (2000b) argued that this muscle is only a secondary subdivision of the pronoto-laterocervical muscle, with its origin shifted from the pronotum to the first phragma. In Scelionidae, the sites of origin of the pronoto-propleural, pronoto-laterocervical, and the pronoto-postoccipital muscles extend along the dorsal margin of the pronotum as well as the first phragma.

### *Mesonotum*

The tegula is connected to the mesoscutum by membranous connectivae. Due to the minute size of dissected specimens we were not able to determine without histologic examinations whether the depressor of the tegula (Duncan 1939) is present or absent from Scelionidae.

The skaphion is a modification of the anterior part of the pronotum that apparently is found in no other family outside of Scelionidae. Kozlov (1970) considered the presence of the skaphion as the main diagnostic character for the tribe Psilanteridini. Masner (1972) argued against this hypothesis, noting that the skaphion is present in a range of other genera, and that its presence or absence was not well correlated with the understanding of higher classification of scelionids. Therefore, he concluded that the "...skaphion is a character of problematic value" (Masner 1972). The skaphion carina, which delimits the posterior margin of the skaphion, crosses the anterior site of attachment of the first phragmo-second phragmal muscle. Therefore, it may be a structure to strengthen the mesoscutum against the stresses generated by muscle contraction. Such stresses, however, are common to almost all flying insects, and this seems to us to be an unsatisfactory hypothesis to explain the development of this region in only a single family of Apocrita. The possible suggestion that the skaphion is a plesiomorphic feature, perhaps the prescutum found widely in other insects, is similarly unsatisfactory because the skaphion is not present in any of the taxa currently considered to be plesiomorphic.

### *Scutellar-axillar complex*

A vertical and a horizontal carina on the axilla in Scelionidae may be homologous with the axillar carina of basal Hymenoptera. The axillar carina separates the vertical dorsal axillar surface from the horizontal lateral axillar surface (Gibson 1985). In Scelionidae, the horizontal

transaxillar carina (tac: Figs 9, 17–19, 75, 77–79, 88, 95, 96) separates a vertical and horizontal area of the axilla, and therefore could be considered as the axillar carina *sensu* Gibson (1985). However, this carina is absent from *Nixonia* (Figs 90, 93) and *Archaeoteleia* (Figs 76, 77); in *Scelio* (Fig. 72) the transaxillar carina seems to be formed secondarily from one of the interspaces between the foveae of the scutoscutellar sulcus. The vertical axillar carina (axc: Figs 9, 17, 18, 76, 77, 79, 88, 90, 91, 93, 95, 96) is well developed in all Scelionidae. It separates an anterior vertical and a posterior partly vertical, partly horizontal area on the axilla. In *Apis* and some other apocritans, mainly in those taxa where the axilla is small, the dorsal axillar area is not only reduced, but is posteriorly or laterally declined. Due to the declination of the dorsal axillar area, the originally horizontal axillar carina then becomes vertical (Gibson 1985). We consider the axillar carina in Scelionidae to be homologous with the axillar carina of other hymenopterans, and thus term the area of the axilla anteriorly delimited by the axillar carina as the lateral axillar area, and the posterior area as the dorsal axillar area. We consider the transaxillar carina to be a new structure in Scelionidae.

Krogmann and Vilhelmsen proposed the term axillular ridge for an oblique internal ridge corresponding to the axillular carina. Similar internal apodeme, the scutellar bridge is present in Telenominae and Teleasinae. However this structure does not correspond to the axillular carina nor other external ridges or carinae. We therefore consider it as a strengthening feature of the mesoscutellum against stresses caused by the contraction of the mesoscutello-metanotal muscle.

The hollow mesoscutellar arm encloses and protect the vein, which connect the reservoir of the dorsal vessel with the wing base. The mesoscutellar arm is well developed in basal Hymenoptera but it is hard to find homologous structure in most Apocrita. Vilhelmsen and Krogmann (2006) defined and locate the mesoscutellar arm in Mymarommatidae, whose lateral part extends to the postalar process (sca: fig. 11). We were not able to detect any hollow structure could be considered as mesoscutellar arm in Scelionidae, however, the vein is hidden by the postalar process prior to reaching the wing base. Therefore we assume, that the postalar process could be the lateral remnant of the scutellar arm in Apocrita.

#### *Mesopectus and mesofurca*

Gibson (1986) reported the retractor of mesoscutum (Figs , 129: pl2-t2c) as present only in Chalcidoidea in Apocrita, but because of its presence in Symphyta hypothesized it as a symplesiomorphy and suggested that the muscle might be found in other apocritans in which the pronotum and mesopleuron were not rigidly connected. He termed the area of the mesopectus serving as site of origin of the retractor of the mesoscutum as the acropleuron.

Ronquist & Nordlander (1989) reported a pleuro-notal muscle in *Ibalia* which ends in a pad of rubberlike material similarly to that in Eupelmidae. They noted, however, that the homology is questionable because the muscle in Eupelmidae inserts more anteriorly than in *Ibalia*. Gibson (1993) homologised the prealary sclerite muscle of *Corydalus* and t2-plr2 muscle of *Xyela* with the retractor of the mesoscutum of eupelmids. In Scelionidae, there is also a muscle similar to that in *Ibalia* and *Xyela* inserting on the ventral apodeme of the first phragma. The apodeme is always located anterior to the preaxilla. Although the muscle originates more anteriorly in eupelmids, the preaxilla is also more elongated anteriorly than in Proctotrupoidea *s. l.* or in Cynipidae, and the muscle originates just anterior to the preaxilla (Gibson 1986: fig. 5). We consider that the muscle reported by Ronquist & Nordlander (1989) in *Ibalia* and that observed in Scelionidae is homologous with the retractor of mesoscutum of *Xyela* and Chalcidoidea. We therefore use the term acropleural apodeme and acropleural sulcus for the apodeme and corresponding external sulcus that serve as the site of origin of the retractor of mesoscutum, or the third mesopleuro-mesonotal muscle (pl2-t2c).

The acetabulum is the anterior, vertical impressed area of the mesopectus limited laterally by the acetabular carina. The acetabular foveae and field (Johnson 1984) are on the anteroventral part of the mesopectus, posterior to the acetabulum; these names were derived on the basis of the proximity of these structures to the acetabulum. In fact, though, they are not part of the acetabulum, and, therefore we prefer to use the adjective postacetabular to refer to them.

Johnson (1984) proposed the term episternal foveae for the sulcus located on the anteroventral part of the mesopectus and used this character for species-group characterizations in *Telenomus*. Some members of other scelionid taxa have similar structures, including Thoronini (Johnson & Masner 2004) and Teleasinae (Mikó & Masner in press). The sulcus corresponds with the mesopleural site of attachment of the mesopleuro-mesobasalar muscle (pl2-ba2) and occurs in most Scelionidae. However, it is usually obscured by the general sculpture of the mesopleuron or is fused with the anterior row of foveae flanking the mesopleural carina. The sulcus is more expressed and separated in taxa having a more extended site of origin of the mesopleuro-mesobasalar muscle. Wharton (2006) revised and homologized some external features of the mesopectus on the basis of muscle attachments in Ichneumonoidea. He redefined the term sternaulus to refer to a sulcus or row of foveae on the mesopleuron corresponding to the mesopleural site of origin of the mesobasalar muscle. Thus, we consider the episternal foveae to be homologous with the sternaulus of Ichneumonoidea and adopt this term for Platygastroidea.

Masner (1976, 1991) and Masner & Huggert (1989) used the term sternaulus for a horizontal carina in *Doddiella* (Scelionidae), and many Platygastriidae and Diapriidae. In Platygastriidae and Diapriidae, the "sternaulus" *sensu* Masner corresponds with the ventral margin of the site of origin of the anterior and posterior mesopleuro-third axillary sclerite of the fore wing muscles and the second mesopleuro-mesonotal muscle, similar to some Cynipidae. This structure is a functional homologue of the precoxal sulcus of Ichneumonoidea (Wharton 2006). In *Doddiella*, however, the second mesopleuro-mesonotal muscle is rodlike and originates from the pleural apodeme. Further, the ventral margin of the site of origin of the two mesopleuro-third axillary sclerite muscles are not aligned at one level. In *Doddiella*, the sternaulus *sensu* Masner does not correspond to the ventral margin of the origin of these muscles, but may correspond with the mesopectal site of attachment of the indirect elevator of the fore wing (first mesopleuro-mesonotal muscle).

The origin of the mesopleuro-mesofurcal muscle extends along the mesepimeral ridge. The dorsal part of the mesopleural site of attachment of the muscle extends to an internally concave, externally convex area on the dorsal part of the mesopectus, which is internally delimited anteriorly by a more or less well-developed apodeme, the anterior margin of the speculum. The anterior margin of the speculum is homologous with the pleural ridge (PIR: fig. 17G of Snodgrass 1942) in *Apis* and with the second mesopleural apodeme (PI2A2: fig. 51 of Duncan 1939) in *Vespula*. Externally, the anterior margin of the speculum corresponds with the prespiracular sulcus, considered here homologous with the pleural sulcus (pls2: Fig. 15 of Snodgrass 1942) in *Apis* and the mesopleural suture (pl2s fig. 42 of Duncan 1939) in *Vespula*. Posteriorly, the site of origin of the mesopleuro-mesofurcal muscle is delimited by the mesepimeral ridge (Ronquist & Nordlander 1989, = k, posterior marginal ridge of mesopleuron, Figs 16H, 17B; Snodgrass 1942, = PI2A3, Fig. 53; Duncan 1939), which corresponds externally to the mesepimeral sulcus (= e, recurrent groove of mesopleuron, Fig. 17A; Snodgrass 1942). The internally concave and externally convex area of the mesopleuron, from which the mesopleuro-mesofurcal muscle originates, is called the speculum in Ichneumonidae (Townes 1969) and Cynipoidea (Ronquist & Nordlander 1989), and we have adopted this term for the Scelionidae. On the basis of muscle attachments, the anterior margin of the speculum is the only internal apodeme in Apocrita, which may be considered as the classical "pleural ridge". This is well developed in all Apocrita and, where complete, it extends between the pleural wing process and the mesocoxal articulation.

In most scelionids the anterior margin of the speculum is reduced ventrally, and the pleural apodeme, if present, is separated from it. In the *Psix* group of genera of Telenominae,

however, the anterior margin of the speculum extends ventrally to the mesocoxal articulation and is indicated externally by the transpleural sulcus (Fig. 105). These structures could be easily considered as homologous with the mesopleural ridge and sulcus of generalized insect which were reported only in Chalcidoidea within Apocrita (Krogmann & Vilhelmsen 2006).

The anterior margin of the speculum is distinctly separated from the pleural apodeme in most Scelionidae. The fusion of the pleural apodeme and the anterior margin of the speculum appears to be unique for the *Trissolcus* and *Telenomus* groups of genera of Telenominae.

The anterior margin of the speculum begins at the posterodorsal edge of the mesopleuron, which corresponds to the subalar pit in Scelionidae. This condition is similar to that in *Vespula*, and therefore we use the term subalar pit (Duncan 1939) instead of posterior subalar pit (Ronquist & Nordlander 1989).

Gibson (1999) discussed the putative evolution of the mesotrochanteral depressor muscles in Hymenoptera. He stated that the muscle originates partly from the mesofurca ( $fu_2$ - $tr_2$ ) and partly from the mesopleuron ( $pl_2$ - $tr_2$ ) in Evaniidae, Peleciniidae, Proctotrupidae and Vanhorniidae, but exclusively from the mesopleuron in Scelionidae. This condition was considered as the end stage of a transformation series in which the tergal origin of the depressor muscle is absent. In those Hymenoptera taxa with only a furcal depressor of the mesotrochanter, the mesofurcal depressor of the mesotrochanter is usually subdivided into a lateral and a median muscle band (Figs 47–49: Gibson 1985). The single depressor muscle of the mesotrochanter in most Scelionidae appears to originate from the surface of the speculum (Gibson 1985, 1999), however, as mentioned above, the speculum is obscured entirely by the origin of the mesopleuro-mesofurcal muscle in all Apocrita. Therefore, the pleural depressor of the mesotrochanter seems to originate from the internal surface of the muscle pad of the mesopleural-mesofurcal muscle (Fig. 10–12, 112, 114). In fact, the membranous anterior extension of the mesofurca serves as the site of origin of both muscles. The anterior extension of the mesofurca is twisted posterodorsally, therefore the originally ventrally located lateral mesofurco-mesotrochanteral muscle originates exclusively from its internal (median) surface, while the originally dorsally located mesopleuro-mesofurcal muscle attaches to its external (lateral) surface (Figs 10–12, 108–115). This condition is widely distributed in apocritans having a pleural depressor of the mesotrochanter *sensu* Gibson (1985, 1999). The lateral band of the depressor of the mesotrochanteral muscle has no pleural origin in Evaniidae, Peleciniidae, Proctotrupidae and Vanhorniidae, but as in Scelionidae originates only from the internal (median) surface of the posterodorsally twisted anterior extension of the mesofurcal. We

assume, that the lateral band of the muscle of these taxa, which was incorrectly considered by Gibson as originating from the pleuron, is homologous with the lateral band of the secondary subdivided furcal depressor of the mesotrochanter of Heloridae, Gasteruptidae and Aulacidae. Therefore, we use the term lateral furcal depressor of mesotrochanter (lateral mesofurco-mesotrochanteral muscle) instead of pleural depressor of mesotrochanter *sensu* Gibson (1985, 1999). In some Scelionidae genera, *Nixonia*, *Sparasion*, *Gryon*, *Idris* and *Archaeoteleia*, both the lateral and the median bands of the furcal depressor of the mesotrochanter are present.

Rasnitsyn (1988) reported that there is no pleural depressor of the mesotrochanter in Platygastriidae. Gibson (1985) also did not find any depressor muscle and proposed two possible explanations for this: (i) the depressor of the mesotrochanter was lost and its function was taken over by one of the coxal muscles or (ii) it is present, but because of the minute size of platygastriids it is difficult to locate. Our dissections show the presence of the lateral furcal depressor of the mesotrochanter in Platygastriidae, and that it appears to originate from the interior surface of the speculum similar to that in Scelionidae and other Hymenoptera. The attachment site of the mesopleuro-mesofurcal muscle is also extended anteriorly lining the interior surface of the speculum as in Scelionidae. A rod like muscle inserts on a tendon from the mesocoxa and originates on the speculum with an extended origin; we consider this to be the lateral furcal depressor of the mesotrochanter in platygastriids.

The mesepimeral ridge, and therefore the corresponding mesepimeral sulcus are epimeral in origin on the basis of the site of origin of the mesopecto-mesofurcal muscle (Ronquist & Nordlander 1989). We therefore do not support the use of the term mesepimeron for the posteriorly delimited area of the mesopectus (e.g., Masner 1979). The postepimeral foveae *sensu* Johnson & Masner (1985) extends on the mesepimeron, and therefore we prefer to use the term mesepimeral sulcus.

Flexors of the hind wing originate exclusively from the metapleuron in most Hymenoptera (Alam 1951, Duncan 1939, Ronquist & Nordlander 1989, Snodgrass 1942, Vilhelmsen 2000a). Gibson (1986) reported that the flexor of the hind wing (pl2-3ax3) originates from the mesopleuron posterior to the mesepimeral ridge in Eupelmidae. Heraty *et al.* (1994) hypothesized that the mesopleural flexor of the hind wing in Eupelmidae could be homologous with the furcal-basalar muscle of some basal Hymenoptera. The flexor of the hind wing originates partly from the posterior mesepimeral area of the mesopectus and partly from the metapectus in *Nixonia*, *Sparasion*, and *Scelio*, but in other scelionids appears to originate exclusively from the mesopectus similar to Eupelmidae. The muscle clearly inserts into the third axillary sclerite of the hind wing. The mesopleural origin of the first flexor of the hind

wing is not unique for Scelionidae and Eupelmidae. The muscle originates at least partly from the mesopleuron also in *Helorus*, *Proctotrupes*, and *Vanhornia*. In those taxa having the mesopleural band of the flexor of the hind wing, the posterior mesepimeral area is well developed. In taxa with the flexor of the hind wing originating only from the metapleuron the mesepimeral ridge usually extends just anterior to the posterior mesepimeral inflection and the posterior mesepimeral area is usually very narrow and inflected. Therefore, we believe that the posterior mesepimeral area of the mesopectus is functionally similar to the netrion and is associated with the transfer of the flexor of hind wing from the metapectus to the mesopectus. In *Apis*, *Proctotrupes*, *Trichopria*, and *Andricus* the mesosubalare muscle originates from the mesocoxa as in Scelionidae. In Chalcidoidea, the muscle originates from the mesopectus.

### *Metanotum*

The term dorsellum is widely used in apocritan taxonomy (e.g., Gibson 1997, Graham 1969, Johnson 1984, Masner & Garcia 2002, Yoder 2004). Ronquist & Nordlander (1989) hypothesized that the dorsellum is homologous with the metascutellum of basal Hymenoptera. Later, Ronquist (1995) reverted to the term dorsellum because of uncertainty whether the structure is serially homologous with the mesoscutellum. Krogmann and Vilhelmsen (2006) synonymized the term dorsellum to metascutellum without explanation. In winged insects, the meso- and metascutellum accommodate circulatory organs connected to the posterior wing veins via the hollow scutellar arms, facilitating circulation of haemolymph through the wings (Krenn & Pass 1994, Vilhelmsen 2000a). The dorsal vessel in the metanotum of Orussidae does not extend to the metascutellum and the scutellar arms are solid (Vilhelmsen 2000a). Vilhelmsen (2000a) hypothesized that this condition may be correlated with the reduced hind wing venation of the family. We assume that because of the reduced hind wing venation of most Apocrita the dorsal vessel is also reduced. The internal metanotal ridge bifurcates medially delimiting the internal chamber of the metanotum in Scelionidae (Figs 126, 127), which corresponds externally with a median, elevated area of the metanotum. This internal chamber is connected to a ventral hollow ridge, which extends along the ventral margin of the metanotum (sca: Figs 126, 127, 132). This condition is similar to that of basal Hymenoptera, where a median chamberlike structure, which corresponds to the metascutellum, is located on the metanotum and is connected with the wing base via the hollow scutellar arm. We assume that the hollow ventral ridge of the scelionid metanotum could be homologous with the scutellar arm and the median elevated area of the metanotum with the metascutellum of basal Hymenoptera. Therefore we use the term metascutellum in preference to dorsellum.

Duncan (1939) reported the presence of an independent, partly or entirely separated sclerite connecting to the anterior margin of the metanotum and bearing the anterior notal wing process. No independent sclerite of the metanotum was reported in basal Hymenoptera (Dhillon 1966, Vilhelmsen 2000a). Ronquist & Nordlander (1989) also did not find any independent sclerite of the metanotum. They assumed that the supraalar area of the Cynipoidea, which bears the anterior notal wing process, could be homologous with the humeral sclerite that is fused secondarily to the metanotum. In Scelionidae, the humeral sclerite is distinctly separated from the metanotum and is connected to the first axillary sclerite of the hind wing similar to that in *Vespula* (Duncan 1939), *Apis* (Snodgrass 1942), and *Stenobracon* (Alam 1951).

Daly (1963) reported presence of the metanoto-metatrochanteral muscle in *Andricus*, *Chalcis*, *Sirex*, and *Xyela*, and that this muscle shares its attachment on the metanotum with the  $t_3$ - $pl_3$  muscle in *Andricus*. Vilhelmsen (2000a) homologized the latter muscle with the median metapleuro-metanotal muscle. The muscle inserts on the humeral sclerite in *Pseudofoenus*, *Pristaulacus*, and *Evaniella* (present observations). The metanoto-metatrochanteral muscle shares its insertion site on the metatrochanter with the metafurco-metatrochanteral muscle, and its origin on the supraalar area with the metapleuro-metanotal muscle in *Andricus* (reported also by Daly 1963). On the basis of the site of metanotal attachment (supraalar area = humeral sclerite), we agree with Vilhelmsen (2000a) that the  $t_3$ - $pl_3$  muscle (Daly 1963) of *Andricus* is homologous with the median metapleuro-metanotal muscle of basal Hymenoptera and Evanoidea. Although in Scelionidae the metanoto-metatrochanteral muscle also originates from the humeral sclerite, it inserts on the metatrochanter via a common tendon with the metafurco-metatrochanteral and the metapleuro-metatrochanteral muscle. The median metapleuro-metanotal muscle is absent. We assume that the median metapleuro-metanotal muscle is secondarily reduced in Scelionidae and consider the metapleuro-metatrochanteral muscle as a secondary subdivision of the metafurco-metatrochanteral muscle.

#### *Metapectal-propodeal complex*

The term epimetrum was proposed by Mineo and Caleca (1992) for a "strongly narrowed vertical and smooth strip, located between the meso and metapleuron" (Figs 1, 2; Mineo and Caleca 1992). On the basis of dissection of *Dyscritobaenus* specimens, the epimetrum is the anterior part of the metapleuron delimited by the fused paracoxal and metapleural sulci. This condition is similar to that in *Sparasion* or *Archaeoteleia*. Therefore we

consider the epimetrum as to be homologous with the anteriorly delimited area of the metapleuron of other Scelionidae.

Vilhelmsen (2000a) concluded that the metapleural ridge and the corresponding metapleural sulcus mark the site of fusion between the metapleuron and the propodeum, and thus the metepimeron is totally reduced in Apocrita. In Scelionidae, however, the metapleural carina usually marks the border between the sites of origin of propodeal and metapleural muscles. A similar carina extends from the metapleural wing articulation to the coxal articulation in *Ibalia* (Ronquist & Nordlander 1989), *Stenobracon* (Alam 1951), *Proctotrupes*, and *Helorus* (present observations). It is difficult to decide whether the metapleural area delimited dorsally by the metapleural carina and ventrally by the metapleural sulcus is homologous with the metepimeron of basal Hymenoptera or is a secondary extension of the metapleuron.

Vilhelmsen (2000a, 2003) considered the anteriorly located metafurca on the metadiscal lamella to an autapomorphy for Hymenoptera. The metafurcal pit is on or close to the posterior end of the metadiscimen and, therefore, the base of the metafurca is located on the posterior part of the metadiscal lamella. However the metafurca is slanted anteriorly and the paracoxal ridge extends posteriorly in most Hymenoptera. Therefore, the metafurcal arms originate anteriorly from the metadiscimen and the metadiscal lamella is triangular from lateral view (Fig. 14b). This condition occurs in most Scelionidae; however, the paracoxal ridge does not extend to the metafurcal arm in Telenomiane, *Idris* and *Gryon* (Figs 14a, 145). Because the former condition occurs in basal Hymenoptera, we consider the posterior site of origin of the metafurcal arms to be a secondary modification.

Four muscles originating from the propodeal-metapleural complex insert on the petiole in Scelionidae. Two of them are clearly homologous with muscles 32 and 35 of basal Hymenoptera (Vilhelmsen 2000a). The other two muscles occur in *Vespula* (Duncan 1939), *Apis* (Snodgrass 1943) and *Stenobracon* (Alam 1951) as the sternal and propodeal rotators of the metasoma. Vilhelmsen (2000a) did not homologize the propodeo-second metasomal tergal muscle with any propodeal muscle of basal Hymenoptera. He also hypothesized that the propodeo-second metasomal sternal muscle could be the secondary subdivision of the metafurco-second abdominal sternal muscle.

**WORLD REVISION OF *XENOMERUS* WALKER (HYMENOPTERA:  
PLATYGASTROIDEA: SCELIONIDAE)**

***Xenomerus* Walker**

*Xenomerus* Walker, 1836: 342, 355.; type species: *Xenomerus ergenna* Walker, 1836, by monotypy.

*Trimorus*: Kononova & Kozlov 2001: 231, 233, 235, 238; Kononova & Petrov 1999: 21, .

For subsequent taxonomic literature see Johnson (1992).

DIAGNOSIS: Male antennomeres A3-A11 bottle shaped, with long, erect, whorled bristles; body short, squat, highly convex, predominantly shining surface with multitude foveolate suture remarkably foveolate; head distinctly transverse, lenticular, always wider than the mesosoma; epicoxal sulcus always foveolate; mandible short, broad, tridentate, with equal teeth; palpal formula 3:1; acrosternal calyx usually fused, spherical in shape; basal striae on T3 usually present; T1 usually trapesiod never with hump.

DESCRIPTION

Female:

*Body length*: 0.58-1.66 mm.

*Colour*: Black to yellow, last tarsomere of all leg darker than preceding, usually interantennal process lighter than head.

*Head*: Transverse almost as high as wide as high; 1.5-2 times as long as high; usually about 1.5 times as wide as inter orbital space, in *X. spinosus* HW/IOS=1.85; inter orbital space usually shorter in or above eye midlevel, in *X. spinosus* inter orbital space shortest below eye midlevel; head 1.2-1.5 times as wide as transscutal line; mandible short and broad with three equal teeth; facial striae short, not exceeding (e.g. Figs 189, 190, 205, 206, 147, 148), or long, extending over (e.g. Fig. 138) and sometimes obscuring frontal patch (e.g. Figs 199, 200, 224, 230, 235), in some cases covering whole frons (e.g. Figs 217, 218); frontal patch distinct (e.g. Figs 186, 187, 202, 203, 244), sometimes exceeding even eye midlevel (Fig. 245), or indistinct, obscured by facial striae and comprising at most an irregular patch below facial striae (e.g. Figs 196, 197, 226, 227); antennal scrobe usually present (Fig 217) in *X. rugifrons* obscured by facial striae (Fig. 218); central keel usually present, incomplete (e.g. Figs 205, 206, 226), or complete (Figs 189, 190, 197-200, 217, 224, 228-230), absent in *X. noyesi*, *X. fulleri* and *X. rugifrons* (Fig. 218); toruli triangle well developed, usually closed, in *X. fulleri* and *X. rugifrons* opened

dorsally (Fig. 215), usually shorter (Figs 189, 190, 197-200, 217, 224, 227-230, 235) in *X. rugifrons* longer (Fig. 215) than clypeus height; POL usually 1-2.5 times as long as OOL, in *X. watshami* and *X. vanharteni* POL about 3 times as long as OOL (Figs 185, 225), in *X. halteratus*, *X. melleus* and *X. rugifrons* POL distinctly shorter OOL (215, 216, 161, 163); vertex patch absent (e.g. Figs 185, 234, 239) or distinct (Figs, 186, 231, 167, 275), sometimes merged with the extended sculpture of the vertex (Figs 187, 188, 215, 216, 225, 227, 276); hyperoccipital carina present, sharp, extending to inner orbit (Fig. 185) or present only between lateral ocelli (Fig. 186), or blunt, extending to inner orbit (Figs 187, 228) or present only between lateral ocelli (Figs 198, 227), or absent (187, 188, 192, 215, 216, 271); genal patch distinct, well segregated from the coriaceous sculpture of vertex (Figs 186, 242) or merges with it (Figs 187, 188, 192) or absent (Fig. 232); hypostomal pit located usually closer to the posterior tentorial pit than to oral foramen, in *X. vanharteni* the hypostomal pit closer to the oral foramen; palpal formula 3:1 (Fig. 254).

*Antenna*: radicle elongated (A1/r=2-3) (Figs 174, 175) or short (A1/r=5-6) (Figs 173, 176); claval formula usually 2:2:2:2:1, 1:2:2:2:1 in *ergenna*-group; A3 usually distinctly shorter than A2 (Figs 173, 175, 176), in *X. spinosus* and *X. rugifrons* A3 as long as A2 (Fig. 174); A1 about as long as clava.

*Mesosoma*: Propleural epicoxal sulcus always foveolate (e.g. Figs 183, 212, 219, 220, 237, 260); propleural cervical sulcus foveolate (e.g. Figs 237, 238) or simple (Figs 212, 260); propleuron scaly reticulate (Figs 212, 219, 220, 237, 260); anterior process of pronotum usually well developed (e.g. Figs 237, 238, 260) in *ochraceus*-group reduced (Fig. 212); pronotal cervical sulcus is foveolate (e.g. Figs 237, 238) or simple (e.g. Figs 219, 220); pronotal suprahumeral sulcus simple (e.g. Figs 219, 260) or foveolate, complete, merged with pronotal cervical sulcus (e.g. Figs 237, 238), or incomplete (e.g. Fig. 212); epomial carina well developed (e.g. Fig. 221) or absent (e.g. Figs 183, 212, 219); posterior pronotal sulcus present, with row of setae; netrion sulcus present, complete (e.g. Figs 183, 219, 220), incomplete (Fig. 237) or absent (212, 221, 238); sometimes netrion sculpture strongly extending to pronotum (Figs 220, 256, 257); netrion usually spindle like, in *X. darlingi* elongated with almost parallel sides (Fig. 256); mesonotal suprahumeral sulcus foveolate, not extending to antero-admedian line (e.g. Figs 186-188, 197, 242); mesonotal humeral sulcus usually foveolate (Figs 237, 238), in *X. vanharteni* both sulci simple, without foveae (Fig. 185); notaulus elongate, almost reaching anterior margin of mesoscutum (e.g. Figs 186, 191, 192), normal, almost reaching transscutal line (e.g. Figs 215, 216, 222), short, not reaching *transscutal line* (Figs 225) or absent in *X. vanharteni* (Fig. 185) and in *ochraceus* group (Fig. 203); mesoscutum with

posteriorly diminishing scaly reticulate sculpture, usually not reaching posterior margin, with rare (Figs 191, 192, 225, 227) or dense (Figs 203, 215, 216, 222) setae, sometimes setal base pustulate resulting coriaceous like sculpture (Figs 215, 239, 255); mesoscutellum transverse, 1.7-2.5 times as wide as long; usually simple, in *X. spinosus* and *X. armatus* with median spine (Fig. 195); mesoscutellum with rare marginal setae (Figs 185-188, 234), in some species all over setaceous (Figs 215, 222); scutoscutellar sulcus foveolate, slightly (Figs 234, 239) or distinctly (Figs 238, 242, 249) diminishing medially, extending onto axillula; trans axillar carina present, merged with axillular carina; posterior scutellar sulcus foveolate, usually extending onto axillula (Fig. 195); subalar pit well developed; acropleural sulcus well developed, sometimes almost reaching anterodorsal edge of mesopleuron (Fig 237, 238); prespecular sulcus and mesepimeral sulcus not merging on speculum; pleural pit well developed; *mesopleural epicoxal sulcus* foveolate; sternaulus usually not separated from anterior row of foveae of mesopleural carina (Figs 237, 238), sometimes well separated (Fig. 256-258); postacetabular sulcus foveolate, postacetabular patch present; mesopleural carina usually complete with complete rows of foveae (Figs 237, 238), sometimes incomplete (Figs 183, 257-259) in *X. vanharteni* almost entirely reduced (Fig. 184); mesepimeral sulcus foveolate, extending to mid coxa; metanotal trough foveolate; metascutellum striated basally; metanotal spine bluntly triangular, basal striation of metascutellum extending to metanotal spine (Figs 203, 215, 263, 264), or with apical semitransparent lamella (Figs 187, 188, 192) or pointed; reduced (Figs 237, 239) or well developed (Figs 238, 240); metapleural pit and sulcus present, upper and lower part foveolate; metapleural epicoxal carina present, extending parallel with the meso-metapleural suture, merging dorsally with vertical part of metapleural sulcus (Figs 237, 238) or with the meso-metapleural suture (*ergenna* group; Figs 183, 184); sulcus along metapleural carina foveolate (Fig. 183) or simple, without any foveae (Fig. 258); plica usually absent, in *X. vanharteni* present; propodeal lateral carina well developed inverted V or Y shaped, shafts straight (e.g. Fig. 211), slightly curved outward or inward or S-shaped (*ochraceus* group; e.g. Fig. 204); metasomal depression and lateral propodeal area striated at least along margins (e.g. Figs 204, 211), marginal striation sometimes extending medially, obscuring propodeal lateral area entirely; posterior propodeal projection absent (e.g. Figs 204, 211), tubercle like or well developed (e.g. Figs 233, 255).

*Wings:* Forewing wider or slightly narrower than mesoscutum; marginal vein 2-3 times as long as stigmal vein; marginal ciliae of hind wing elongated, hind wing usually less than 2 times as wide as marginal ciliae length, much shorter only in *X. darlingi*.

*Metasoma*: Metasoma transverse, usually circular in shape, T3 as wide or slightly wider than mesoscutum; T1 with 2 lateral setae; basal grooves on T1 and T2 present, T1 usually concave in lateral view, in *X. malawi* slightly convex; lateral patch on T2 distinct (e.g. Figs 193, 194) or indicated only by a few setae (e.g. Figs 197, 209, 210); basal grooves on T3 usually present (e.g. Figs 193, 194, 209, 210, 213, 214), in *X. darlingi*, *X. noyesi* and *X. vanharteni* absent (Figs 253, 254); usually costae erecting from *basal grooves*, sometimes almost reaching posterior margin (Figs, 251, 252), sometimes T3 longitudinally rugulose (Figs 196, 223); lateral patch on T3 present (e.g. Fig. 196) or absent; posterodorsal patch on T3 present, sometimes obscured by basal sculpture of tergum (e.g. Fig 213); basal grooves present on S1,S2. If basal grooves present on T3, than present on S3 (Figs 281-288); lateral and median patches on T4 usually present, not fused (e.g. Figs 214, 251, 252) median patch sometimes absent or marked by punctures (e.g. Fig. 253), sometimes anterior part of T4 entirely reticulate (e.g. Fig. 196), in *X. vanharteni* T4 smooth; felt field present; posterior felt field present in males, acrosternal calyx fused and circular in shape (*comatus*- and *ergenna*-groups Figs 280, 283-288), circular in shape but well separated (*ochraceus*-group Fig. 284) or ovoid, transversely elongate and well separated (*melleus*-group Figs 279, 281, 282); T7+8 with two (*ergenna*-group) or 4 apical setae; median extensions of *lateral* apodemes are separated, slightly converging (Fig. 188), proximal part of ventral membranous plate simple, without rod like structure anteriorly, median apodeme present on S6.

#### Male:

Differs from female in wider and shorter head, sometimes almost 1.5 times as wide as high (*X. melleus*, Fig. 261); *inter orbital space* shortest below eye midlevel; antennomeres distinctly narrowing apically forming neck like constriction and eventuating bottle like shape of antennomeres (Figs 169-172, 177-180); A6-A11 (Figs 179, 180) or A7-A11 (Figs 169, 170, 177) or A8-A11 (Fig. 171) with stronger (Fig. 177) or weaker (Fig. 180), distinct median constriction (dibottled) and two whorls of setae or without constriction (unibottled) and one whorls of setae (Fig. 178); number of ventral microcilia on male A3-A11 1-3 (few) (Figs 170, 171, 177-180) or 6-10 (numerous) (Figs 169, 172); A5 distinctly modified (Figs 171, 179, 180) or not modified (Figs 169, 170, 172); notaulus present.

#### COMMENTS

The only autapomorphy of *Xenomeres* is the bottle shaped male antennomeres (A3-A11).

The original concept of *Xenomerus*, the „bottle shape” male antennomeres with whorls of erect long bristles established by Walker (1836: “Antennae...verticillato-pilosae...”), was widely accepted by subsequent authors and play important role for the tribal classification of Teleasinae (Kozlov 1970, Masner 1976, Austin & Field 1997). However, this type of male antennae occurs in many other Hymenoptera taxa, *Acanthopria* and *Trichopria* in Diapriidae (Proctotrupoidea); Eurytomidae and Pteromalidae (Chalcidoidea) and *Ipitrachelus* and *Allotropa* from the other platygastroid family, the Platygastriidae. It is undisputed that the developing of bottle shape antennomeres in different superfamilies or families was eventuated by parallel evolution. The distal or/and proximal part of antennomeres is neck like, elongated and the median broader part „body” is bearing whorl (or whorls) of erect, long bristles. This structure of antennae might be important in the detection and/or coordination of fly speed and direction through Johnston’s organ located in the thickened apical part of A1 (Chapman 2001).

We have found one new genus of Teleasinae (*Gen. n.*) from the Neotropical region having bottle shape antennomeres with erect bristles and mandible with three equal teeth; nevertheless differ in many characters from the concept of *Xenomerus* we are proposing in this paper. *Gen. n.* has median ridge on mesonotum (Fig. 277), which is unique in Teleasinae, type of mesopleuron (Fig. 278) typical to a species group of *Trimorus* around *T. varicornis* (Thomson 1859), absence of beak like extension and anterior tip of pronotum and areolate rugulous mesoscutellum like in members of *Teleas* group of genera (Masner 1976). There are also massive differences in the ovipositor system. Austin and Field (1997) described the ovipositor system of Teleasinae, and differentiated five types for the subfamily. On the basis of own observations the ovipositor, T7+8 and lateral apodemes (Fig. 182) of *Xenomerus* species fit to the diagnoses of *Trimorus* ovipositor provided by Austin and Field (1997): the lateral extensions of lateral apodemes are not fork like (fork like only in *flavipes*-group of *Trimorus*; own observation) but connect to S6 separately, whereas the description of the ovipositor system given for *Xenomerini* by Austin and Field (1997) is fit well the ovipositor and T7+8 with lateral apodemes (Fig 181) of *Gen. n.*

Besides the above mentioned differences between *Xenomerus* and *Gen. n.*, the fusion of acrosternal calyx and the concentration level of intersternal muscles between S4 and S5 is similar to that in most *Xenomerus* species.

Based on the ovipositor system and other external characters, *Xenomerus* clearly belongs to *Trimorus* clade of Teleasinae (Masner, 1976). The main diagnostic character of *Xenomerini*, the bottle shaped male antennomeres occur in some other species on *Trimorus* clade (*flavipes*-group) and could develop parallel during the evolution. Therefore, we do not

support to use the tribal classification of Teleasinae proposed by Kozlov (1970) and consider *Xenomerus* in the *Trimorus* group of genera (Masner 1976).

Accordingly, the structure of the male antenna as the single limit of *Xenomerus* is not enough for accurate and correct generic definition.

### **Species-groups of *Xenomerus*:**

The *ergenna*-group

DIAGNOSIS: male antennomeres without median constriction (“unibottled”), with few ventral microcilia; A5 modified; claval formula: 1:2:2:2:1; suprahumeral and cervical pronotal sulci not foveolate; anterior tip of pronotum well developed; notaulus usually present in females, in *X. vanharteni* absent both in males and females; mesopleural carina incomplete; metapleural epicoxal carina merging with the meso-metapleural suture below the level of metapleural sulcus; propodeal lateral carinae inverted V-shaped; lateral patch on T3 reduced, not extending to the whole tergum; apical setae on T3 normal, not elongated; S8 with two apical setae; acrosternal calyx separated, spherical in shape;

INCLUDED SPECIES: *X. buccatus* (Kononova & Kozlov), *X. calligetis* (Kononova & Kozlov), *X. canariensis* Huggert, *X. cornutus* (Kononova & Kozlov), *X. ergenna* Walker, *X. indicus* Mukerjee.

HOSTS: Dromiinae, *Xenomerus ergenna* Walker (Bin, 1981)

DISTRIBUTION: Palaearctic, Oriental and Ethiopian

The *melleus*-group (present designation)

DIAGNOSIS: male A7-A11 with weak median constriction (“dibottled”), with few ventral microcilia; A5 modified; claval formula: 2:2:2:2:1; suprahumeral and cervical pronotal sulci not foveolate; anterior tip of pronotum well developed; notaulus present in female; mesopleural carina complete or incomplete; metapleural epicoxal carina merging dorsally with the vertical part of metapleural sulcus; propodeal lateral carinae inverted V-shaped; lateral patch on T3 extending to the whole tergum; apical setae on T3 normal, not elongated; S8 with 4 apical setae; acrosternal calyx transversely elongated, well separated.

INCLUDED SPECIES: *X. halteratus* Mikó et Masner., *X. melleus* Mikó et Masner

HOSTS: unknown

DISTRIBUTION: Australia: Queensland, Victoria

The *ochraceus* group (present designation)

DIAGNOSIS: male A7-A11 with weak median constriction (“dibottled”), with numerous ventral microcilia; A5 modified; claval formula: 2:2:2:2:1; suprahumeral pronotal sulcus foveolate, cervical pronotal sulcus simple; anterior tip of pronotum reduced; notaulus absent in female; mesopleural carina complete; metapleural epicoxal carina merging dorsally with the vertical part of metapleural sulcus; propodeal lateral carinae “S” shaped; lateral patch on T3 reduced, not extending to the whole tergum; apical setae on T3 elongated  $T3l/asT3=1.5$ ; S8 with 4 apical setae; acrosternal calyx separated, spherical in shape.

INCLUDED SPECIES: *X. guinensis* Mikó et Masner, *X. ochraceus* Mikó et Masner, *X. yamagishii* Mikó et Masner

HOSTS: unknown

DISTRIBUTION: Ethiopian, Oriental and Palearctic (Japan).

The *comatus* group (present designation)

DIAGNOSES: male A7-A11 without median constriction or with strong median constriction (“unibottled” or “dibottled”), with few or numerous ventral microcilia; A5 modified or simple; claval formula: 2:2:2:2:1; suprahumeral sulcus foveolate; cervical pronotal sulcus, except *X. rugifrons* foveolate; anterior tip of pronotum well developed; notaulus present; mesopleural carina complete or incomplete; metapleural epicoxal carina merging dorsally with the vertical part of metapleural sulcus; propodeal lateral carinae inverted V- or Y shaped; lateral patch on T3 reduced, not extending to the whole tergum; apical setae on T3 short; S8 with 4 apical setae; acrosternal calyx fused, spherical in shape.

INCLUDED SPECIES: *X. armatus* Mikó et Masner, *X. aureipes* Mikó et Masner, *X. bickeli* Mikó et Masner, *X. comatus* Mikó et Masner, *X. darlingi* Mikó et Masner, *X. laticeps* Dodd, *X. forax* Kozlov & Lé, *X. fragilis* Mikó et Masner, *X. fulleri* Mikó et Masner, *X. gloriosus* Mikó et Masner, *X. guinensis* Mikó et Masner, *X. halteratus* Mikó et Masner, *X. hilleri* Mikó et Masner, *X. kalocsai* Mikó et Masner, *X. feehani* Mikó et Masner, *X. laticeps* Dodd, *X. madag* Mikó et Masner, *X. malawi* Mikó et Masner, *X. melikai* Mikó et Masner, *X. melleus* Mikó et Masner, *X. noyesi* Mikó et Masner, *X. ochraceus* Mikó et Masner, *X. orientalis* Mikó et Masner, *X. paraorientalis* Mikó et Masner, *X. rugifrons* Mikó et Masner, *X. scutellatus* Mikó et Masner, *X. solox* Kozlov & Lé, *X. spinosus* Mikó et Masner, *X. vanharteni* Mikó et Masner, *X. varipes* Dodd, *X. watshami* Mikó et Masner.

HOSTS: Dromiini (*X. orientalis* sp. n.)

DISTRIBUTION: Ethiopian, Oriental and Australian.

On the basis of remained body parts and original description *X. indicus* belongs into *ergenna*-group and could be conspecific with *X. canariensis*. *X. solox* and *X. forax* belong to *comatus*-group, and could be conspecific with *X. orientalis*.

### Key to world species of *Xenomerus*

FEMALES (Unknown for *X. darlingi*, *X. fragilis*, *X. fulleri*, *X. hilleri*, *X. madag*, *X. melleus*, *X. noyesi*.)

- 1 Mesopleural carina incomplete, not extending down to mesocoxa (Fig. 183) or carina entirely absent (Fig. 184) (*ergenna*-group). **2**
  - Mesopleural carina complete, extending down to mesocoxa (e.g. Figs 212, 219, 221). **7**
- 2(1) Keel like hyperoccipital carina extending to inner orbit (Fig. 185); notaulus absent (Fig. 185); mesopleural carina absent, sulci on mesopleuron not foveolate (Fig. 184); T3 without basal grooves; Yemen. *X. vanharteni* sp. n.
  - Hyperoccipital carina, if keel like, not extending to inner orbit (e.g. Figs 186-188, 191, 192); notaulus present (Fig. 186-188, 191, 192); mesopleural carina present, sulci on mesopleuron foveolate (Fig. 189); T3 with basal grooves (e.g. Figs 193, 194). **3**
- 3(2) **POL** 2-2.2 times as long as **OOL**; vertex behind **POL** unsculptured, with sharp hyperoccipital carina (Fig. 186); Old world, widespread. *X. ergenna* Walker
  - **POL** 1.0-1.4 times as long as **OOL**; vertex behind **POL** sculptured, hyperoccipital carina absent (e.g. Figs 187, 188, 191, 192). **4**
- 4(3) Wings reduced, forewing not longer than mesoscutum; mesoscutum 2.5 times as wide as long; mesosoma yellowish (Fig. 187); Russia. *X. buccatus* (Kononova & Kozlov)
  - Wing developed, longer than body length; mesoscutum 1.4-1.6 times as wide as long; mesosoma blackish (Figs 188, 191, 192). **5**
- 5(4) Sculpture of vertex extending down to frons (Fig. 189); mesoscutum sculpture reaching posterior margin (Fig. 188) (metasoma elongate, T1 3-3.5 times as wide as long); Russia, Netherlands. *X. calligetus* (Kononova & Kozlov)
  - Frons smooth (Fig. 30) sculpture of mesoscutum not reaching posterior margin (e.g. Figs 191, 192). **6**
- 6(5) Sculpture of vertex merging with genal patch, cells of reticulate sculpture as wide as lateral ocellus diameter; **POL=OOL** (Fig. 192); notauli less converge, shortest distance between notauli (DPN) two times as long as between posterior end of notaulus and posterolateral edge

- of mesoscutum (DNP) (Fig. 192); metasoma elongated: **T1** 3-3,5 times as wide as long (Fig. 194); **A1** 1.4 times as long as radicle; Russia (Primorskiy Kraj), Japan. *X. cornutus* (Kononova & Kozlov)
- Sculpture of vertex not reaching genal patch, cells of reticulate sculpture half as wide as lateral ocellus diameter; **POL/OOL**=1.3-1.5 (Fig. 191); shortest distance between notauli (DNP) as long as distance between posterior end of notaulus and posterolateral edge of mesoscutum (DNP) (Fig. 191); metasoma short: **T1** 5,5-6 times as wide as long (Fig. 193); **A1** 3-3.2 times as long as radicle; Old world, widespread. *X. canariensis* Huggert
- 7(1) Mesoscutellum medially with sharp spine (Figs 195, 202) and median keel extending between anterior margin and apex of spine (**T3** longitudinally rugoso-punctate (Fig. 196). **8**
- Mesoscutellum unarmed (e.g. Figs 203, 215, 216). **9**
- 8(7) Hyperoccipital carina not extending to inner orbit; vertex patch present (Fig. 198); **HW/IOS**=1.8, **IOS** longest below eye midlevel (Fig. 200); netrion sulcus present (Fig. 201); **A4** distinctly longer than **A3**; Taiwan, Malaysia. *X. spinosus* sp. n.
- Hyperoccipital carina extending to inner orbit; vertex patch absent (Fig. 197); **HW/IOS**=1.5, **IOS** longest above eye midlevel (Fig. 199); netrion sulcus absent; **A4** distinctly shorter than **A3**; Thailand. *X. armatus* sp. n.
- 9(7) Notaulus absent (Fig. 203); propodeal lateral carina S shaped (Fig. 204); **T3** with elongated apical setae (Fig. 208-210) (*ochraceus*-group). **10**
- Notaulus present (e.g. Figs 215, 216, 222, 225), propodeal lateral carinae inverted Y or V shaped (Fig. 211); apical setae on **T3** not elongated (e.g. Figs 213, 214, 223, 236). **12**
- 10(9) Frons with dense setae (Fig. 205, 207); **T3** costae extending at most to middle of tergum (Fig. 208, 209); if mesoscutellum and head black, mesonotum black. **11**
- Frons with rare setae (Fig. 206); **T3** costae exceeding middle of tergum (Fig. 210); mesoscutellum and head black, mesonotum yellowish; Papua New Guinea. *X. guinensis* sp. n.
- 11(10) Central keel incomplete (Fig. 205); basal grooves on **T3** thick (Fig. 209); **POL/OOL**=1.25-1.35; *Ethiopian, Oriental. X. ochraceus* sp. n.
- Central keel complete (Fig. 207); basal grooves on **T3** thin (Fig. 208); **POL/OOL**= 1.0-1.15; Oriental. *X. yamagishii* sp. n.
- 12 (9) **POL** distinctly shorter **OOL** (**POL/OOL**=0.64-0.8) (Figs 215, 216); facial striae extending to vertex sculpture, frons with rugulous sculpture (Figs 217, 218). **13**
- **POL** equal or longer **OOL** (**POL/OOL**=1.0-3.41) (e.g. Figs 222, 225, 227, 228, 231, 239); frons without rugulous sculpture (if facial striae extending to **OOL**, frons not rugulous) (e.g. Figs 224, 226, 229, 230). **14**

- 13(12) **T3** costae not exceeding middle of tergum, posteriorly reticulate (Fig. 213); pronotal suprahumeral sulcus not foveolate; netrion sculpture not extending onto lateral pronotal area (Fig. 219); metascutellum blunt triangular, entirely striated; wings reduced, slightly longer than mesosoma (Fig. 215); radicle short ( $A1/r=6-6.46$ ) (Fig. 173, 217); Australia. *X. halteratus* sp. n.
- **T3** costae reaching posterior margin of tergum, posteriorly not reticulate (Fig. 214), pronotal suprahumeral sulcus foveolate; netrion sculpture extending to propleuron (Fig. 220); metascutellum pointed, only base striated (Fig. 216); wings well developed, longer than body length; radicle elongated ( $A1/r=2.7-2.8$ ) (Figs 174, 218); Indonesia, Malaysia. *X. rugifrons* sp. n.
- 14(12) **T3** longitudinally rugoso-punctate (Fig. 223); frons and mesonotum with dense, thick setae (Fig. 222, 224) (netrion sulcus absent; anterior and posterior row of foveae of mesopleural carina complete (Fig. 221); radicle distinctly elongate:  $A1/radicle= 2.3-2.8$ ); Africa, widespread. *X. comatus* sp. n.
- **T3** with only longitudinal costae (Figs 271, 272), frons with rare, thin setae (e.g. Figs 227-230, 235, 241, 247, 248). **15**
- 15(14) **POL** about 3 times as long as **OOL** (2.9-3.4), **LOL** > **OOL** (Fig. 225) (Notaulus short, not reaching transscutal line (Fig. 225); netrion sulcus present; vertex reticulate behind **POL** (Fig. 225); central keel incomplete (Fig. 226); Africa, widespread; United Arab Emirates. *X. watshami* sp. n.
- **POL** 1.0 to 2.2 times as long as **OOL** (1.02-2.23), **LOL** longer **OOL** (e.g. Figs 227, 228, 239, 240, 242, 245, 249, 250). **16**
- 16(15) Radicle elongate:  $A1/r=2.76-3.4$  (e.g. Fig. 175); metasoma less elongated ( $T1W/T1+2=1.8-1.9$ ). **17**
- Radicle short:  $A1/r=5-6.5$  (e.g. Fig. 176); metasoma more elongated ( $T1W/T1+2=1-1.4$ ). **19**
- 17(16) Hyperoccipital carina extending to inner orbit; vertex smooth (Fig. 228); facial striae extends middle of frons curved to central keel (Fig. 230); mesoscutellum anteriorly rugulose (Fig. 267); **T3** costae almost reaching posterior margin submedially strongly reduced, not exceeding 1/3 tergum medially and laterally ( $POL/OOL=1.38-1.77$ ); Oriental, widespread. *X. orientalis* sp. n.
- Hyperoccipital carina not extending to inner margin of eye, vertex patch present (Fig. 227); facial striae never extends middle of frons not curved to central keel (e.g. Fig. 227); mesoscutellum smooth (Fig. 231); costae on **T3** distinctly exceeding middle of tergum submedially. **18**

18(17) Vertex smooth, only vertex patch present (Fig. 231); genal patch absent (Fig. 232); **POL/OOL=1.7-1.8** (Fig. 231); **A1/r=2.7-2.8** (Fig. 175); lateral pronotal area without sculpture; South Africa, Kenya. *X. aureipes* sp. n.

- Vertex entirely reticulate (Fig. 227); genal patch present; **POL/OOL=2.1-2.2** (Fig. 227); **A1/r=3.3**; lateral pronotal area with oblique crenulae; Brunei, Vietnam. *X. paraorientalis* sp. n.

19(16) Mesoscutellum anteriorly rugulous (Fig. 233), (**POL/OOL=1.2**, **OOL/LOL=1.7**); Uganda. *X. scutellatus* sp. n.

- Mesoscutellum smooth (e.g. Figs 234, 239, 240, 242, 245) or crenulated anteriorly (Fig. 246).

## 20

20(19) Mesoscutellum anteriorly with transverse rugae (Fig. 246); dorsal margin of T1 convex from lateral view (**POL=OOL**, **OOL/LOL=1.36**; facial striae not exceeding frontal patch, not parallel with inner orbit; central keel incomplete; T3 costae exceeding 2/3 of tergum); Malawi. *X. malawi* sp. n.

- Mesoscutellum smooth anteriorly (Figs 234, 239, 240, 242, 245, 249, 250); dorsal margin of T1 concave from lateral view. **21**

21(20) Notaulus not reaching transscutal line, 2-3 times as long as wide (Fig. 234) (**OOL=POL**; **OOL/LOL=2**; vertex smooth, facial striae exceeding frontal patch, parallel with inner orbit; central keel complete; T3 costae not exceeding middle tergum); Papua New Guinea. *X. melikai* sp. n.

- Notaulus reaching transscutal line, 8-10 times as long as wide (Figs 239, 240, 242, 245, 249, 250). **22**

22(21) Facial striae exceeding eye midlevel, parallel with inner orbit; central keel complete (Figs 235, 241); T3 costae not exceeding middle tergum (e.g. Fig. 236). **23**

- Facial striae not exceeding eye midlevel, not parallel with inner orbit; central keel incomplete (Figs 247, 248); T3 costae exceeding 2/3 of tergum (Figs 251, 252). **26**

23(22) Eye widest below midlevel (frontal view) (Fig. 241); scutellum less transverse (**SW/SL=1.8**) (Figs 242, 245); T3 as long as wide. **24**

- Eye widest in midlevel (Figs 235); scutellum transverse (**SW/SL=2-2.2**) (Figs 239, 240); T3 about 1.5 times as wide as long. **25**

24(23) Metascutellum unarmed (Fig. 242); netrion enlarged, distinctly wider than fore coxa (Fig. 243); Australia, Queensland. *X. gloriosus* sp. n.

- Metanotal spine well developed (Fig. 245); netrion smaller, as wide as fore coxa (Fig. 244); Australia, Victoria. *X. bickeli* sp. n.

25(23) Metanotal spine long, slender (Fig. 238, 240); netrion sulcus absent, netrion larger (Fig. 238); mesonotum finely reticulate (Fig. 240); antenna brown; vertex patch present; Australia *X. laticeps* Dodd

- Metanotal spine short, tubercle like (Figs 237, 239); mesoscutum granulose like (Fig. 239); netrion sulcus present, netrion smaller (Fig. 237); A1-A6 yellow, clava brown; vertex patch absent; Australia, Queensland *X. varipes* Dodd

26(22) **POL=OOL** (Fig. 250), frontal patch as wide as long, not reaching eye midlevel (Fig. 247), metasoma shorter ( $T1W/T1+2L=1.21$ ); T3 posteriorly with coriaceous sculpture (Fig. 252); coxae yellow; Africa. *X. feehani* sp. n.

- **POL/OOL=1.4** (Fig. 249); frontal patch vertically elongated, exceeding eye midlevel (Fig. 248); metasoma longer ( $T1W/T1+2L=1.4-1.5$ ); T3 posteriorly smooth (Fig. 251); coxae brown Africa. *X. kalocsai* sp. n.

MALES (Unknown for *X. armatus*, *X. bickeli*, *X. buccatus*, *X. feehani*, *X. gloriosus*, *X. guinensis*, *X. halteratus*, *X. kalocsai*, *X. malawi*, *X. melikai*, *X. paraorientalis*, *X. rugifrons*, *X. scutellatus*, *X. spinosus*)

1 A8-A11 without median constriction (e.g. Fig. 178). **2**

- A8-A11 with median constriction (e.g. Fig. 177). **10**

2(1) Notaulus absent (Fig. 185); mesopleural carina absent, sulci on mesopleuron not foveolate (Fig. 184); vertex with sharp hyperoccipital carina extending to inner orbit (Fig. 185) (T3 smooth); Yemen. *X. vanharteni* sp. n.

- Notaulus present (e.g. Figs. 186-188, 191, 192); mesopleural carina present, sulci on mesopleuron foveolate (e.g. Figs. 183, 257, 258). **3**

3(2) **T3** smooth (Fig. 253) (sculpture of netrion extending to propleuron (Fig. 257); Indonesia. *X. noyesi* sp. n.

- **T3** sculptured (e.g. Figs 251, 252, 254). **4**

4(3) **T3** without basal grooves (Fig. 254); mesoscutum granulose; mesoscutellum granulose anteriorly; vertex with transverse rugae (Fig. 255); netrion with parallel sides (Fig. 256) (netrion striation extending to pronotum, netrion sulcus present); Vietnam. *X. darlingi* sp. n.

- **T3** with basal grooves (e.g. Figs. 193, 194); mesoscutum scaly reticulate; mesoscutellum smooth (Figs 186-188, 191, 192); vertex and occiput without transverse rugae (e.g. Figs 263, 264, 270, 271, 275, 276). **5**

- 5(4) Netrion sulcus absent, sculpture of netrion extending to propleuron (e.g. Fig. 257); Thailand. *X. fulleri* sp. n.
- Netrion sulcus well developed, sculpture of netrion not extending to propleuron (e.g. Figs 183, 259). **6**
- 6(5) Metapleural carina not merging with meso-metapleural suture; pronotal cervical and suprahumeral sulcus foveolate, sternaulus distinctly separated from anterior row of foveae of mesopleural carina (Fig. 258); Madagascar. *X. madag* sp. n.
- Metapleural carina merging into meso-metapleural suture (e.g. Fig. 183); pronotal cervical and suprahumeral sulcus not foveolate; sternaulus not separated from anterior row of foveae of mesopleural carina. **7**
- 7(6) **POL** 2-2.2 times as long as **OOL**; vertex behind **POL** unsculptured, with sharp hyperoccipital carina (Fig. 186); Old world, widespread. *X. ergenna* Walker
- **POL** 1.0-1.4 times as long as **OOL**; vertex behind **POL** sculptured; hyperoccipital carina absent (e.g. Figs 186-188, 191, 192). **8**
- 8(7) Sculpture of vertex extending down to frons (Fig. 189); mesoscutum sculpture reaching posterior margin (Fig. 188) (metasoma elongate, T1 3-3,5 times as wide as long); Russia, Netherlands. *X. calligetus* (Kononova & Kozlov)
- Frons smooth (Fig. 190) sculpture of mesoscutum not reaching posterior margin (e.g. Figs 191, 192). **9**
- 9(8) Sculpture of vertex merging with genal patch, cells of reticulate sculpture as wide as lateral ocellus diameter; **POL=OOL** (Fig. 192); notauli less converge, shortest distance between notauli (DPN) two times as long as between posterior end of notaulus and posterolateral edge of mesoscutum (DNP) (Fig. 192); metasoma elongated: T1 3-3,5 times as wide as long (Fig. 194); A1 1.4 times as long as radicle; Russia (Primorskij Kraj), Japan. *X. cornutus* (Kononova & Kozlov)
- Sculpture of vertex not reaching genal patch, cells of reticulate sculpture half as wide as lateral ocellus diameter; **POL/OOL=1.3-1.5** (Fig. 191); shortest distance between notauli (DPN) as long as distance between posterior end of notaulus and posterolateral edge of mesoscutum (DNP) (Fig. 191); metasoma short: T1 5.5-6 times as wide as long (Fig. 193); A1 3-3.2 times as long as radicle; Old world, widespread. *X. canariensis* Huggert
- 10(1) A7 without median constriction (Fig. 171) (mesopleural carina incomplete (Fig. 259)); Botswana, Malawi. *X. fragilis* sp. n.
- A7 with median constriction (e.g. Figs 177, 179, 180). **11**

- 11(10) T3 longitudinally rugoso-punctate (Fig. 223), frons with dense, thick setae (Fig. 224); (OOL 1.5 times as short as POL; netrion sulcus absent; genal patch present; antennomeres with few ventral microcilia). *X. comatus* sp. n.
- T3 with only longitudinal costae (e.g. Figs 236, 251, 252); frons with thin, short setae (e.g. Figs 261, 262, 272). **12**
- 12(11) Metascutellum bluntly triangular, entirely striated (Figs 263, 264); pronotal cervical sulcus not foveolate (e.g. Figs 260); mesosoma light brown to yellow; median constrictions on male antennomeres weak (Figs 172, 179, 180). **13**
- Metascutellum pointed, only base striated (Fig. 267, 268, 270, 271, 275, 276); mesosoma dark brown to black; pronotal cervical sulcus foveolate (Figs 268, 276); median constriction of male antennomeres distinct (Fig. 177). **15**
- 13(12) Mesopleural carina incomplete; netrion sulcus present (Fig. 265); pronotal suprahumeral sulcus absent (Fig. 260); facial striae exceeding top of head (Fig. 261); mesoscutellum anteriorly sculptured (Fig. 263); A4-6 with few ventral microcilia (Fig. 280); apical setae on T3 short. Australia. *X. melleus* sp. n.
- Mesopleural carina complete, netrion sulcus absent, pronotal suprahumeral sulcus present (Fig. 212); head less transverse, facial striae not exceeding top of head (Fig. 262); mesoscutellum smooth (Fig. 264); A4-6 with numerous ventral microcilia (Fig. 172); T3 apical setae elongated (Fig. 208-210). **14**
- 14(13) Central keel complete (Fig. 207); basal grooves on T3 thin (Fig. 208). Japan. *X. yamagishii* sp. n.
- Central keel incomplete (Fig. 205, 262); basal grooves on T3 thick (Fig. 209). *X. ochraceus* sp. n.
- 15(12) Mesopleural carina incomplete; netrion distinctly wider than fore coxa (Fig. 269) (head widest below midlevel (Fig. 266); netrion sulcus complete (Fig. 269); Australia, Queensland. *X. hilleri* sp. n.
- Mesopleural carina complete; netrion narrower than fore coxa. **16**
- 16(15) POL 2.5-2.7 times as long as LOL, vertex entirely reticulate (Fig. 276); central keel incomplete (Fig. 274); Africa. *X. watshami* sp. n.
- POL 1-1.5 times as long as OOL; vertex smooth behind POL (e.g. Figs 267, 268, 270, 271, 275); central keel complete (Figs 272, 273). **17**
- 17(16) POL/OOL=1.3-1.5; A5 modified (e.g. Figs 171, 180) (Africa, Oriental). **18**
- POL/OOL=1.0; A5 not modified (e.g. Figs 169, 170) (Australia). **19**

18(16) A3-8 with numerous ventral microcilia; genal patch absent; hyperoccipital carina not extending to inner orbit; mesoscutellum smooth (Fig. 275); netrion sulcus complete; facial striae shorter, not curved inward (Fig. 273); T3 costae almost reaching posterior margin submedially; Africa.

*X. aureipes*

- A3-8 with few ventral microcilia; genal patch present; hyperoccipital carina extending to inner orbit; mesoscutellum anteriorly rugulous (Fig. 267); facial striae extending to frons, curved inward (e.g. Fig. 230); T3 costae reduced submedially; Oriental. *X. orientalis* sp. n.

19(18) A3-A7 with numerous ventral microcilia (Fig. 169); metanotal spine reduced, tubercle like (Fig. 270); last tibia and tarsi brown; Australia, Queensland. *X. varipes* Dodd

- A3-A7 with few ventral microcilia (Fig. 170); metanotal spine elongated (Fig. 271); last tibia and tarsi yellow; Australia. *X. laticeps* Dodd

**For descriptions of species see APPENDIX 6.**

## SUMMARY

This thesis is a contribution toward a comprehensive examination of the internal and external morphology of the insect family Scelionidae (Hymenoptera: Platyastroidea). One of the goals is to reconcile the different terms used in the taxonomic literature of this family of parasitoid wasps and to coordinate with the nomenclature used for other groups of Hymenoptera. I seek to provide a precise nomenclature for scelionid anatomy for use in systematics, and thus to contribute to further advances in our understanding of the taxonomy and interrelationships of its constituent groups. Given the enigmatic position of the family in the Apocrita (summarized in Austin et al. 2005), the recognition of homologous characters with other hymenopterans will facilitate work toward a robust phylogenetic hypothesis for the entire order.

### *Morphology of Scelionidae*

The sceleptomusculature of the head and mesosoma of the parasitoid wasp family Scelionidae is reviewed. Terminologies used for other groups of Hymenoptera are compared, and a consensus nomenclature is proposed. External characters are redescribed and their phylogenetic importance is discussed on the basis of corresponding internal apodemes, attaching muscles and putative exocrine gland openings. As the result of this work:

1. 229 skeletal structures were termed and defined, from which 84 were newly established or modified.
2. 67 muscles of the head and mesosoma were described and homologized with those present in other Hymenoptera taxa.
3. The presence of the cranio-antennal muscle, an extrinsic antennal muscle originating from the head capsule, is unique for Scelionidae, all extrinsic antennal muscles of other Hymenoptera originates from the tentorium.
4. The dorsally bented epistomal sulcus and the corresponding internal epistomal ridge extend to the anterior margin of the oral foramen, the clypeo-pleurostomal line is absent and the tentorium is fused with the pleurostomal condyle.
5. The frontal ledge of the frons is present in those scelionid genera having the anterior mandibular articulation located on the lateral margin of the oral foramen. The ledge corresponds to the site of origin of the mandibular abductor muscle, which is replaced from the genal area to the top of the frons.
6. The protractor of the pharyngeal plate originates dorsally of the antennal foramen in

Scelionidae.

7. All scelionid genera have postgenal bridge developed between the oral and occipital foramina.

8. The propleural arm is reduced, thus the site of origin of muscles originate from the propleural arm in other Hymenoptera were transferred to other propectal structures in Scelionidae. The profurcal bridge is absent and two profurcal pits are developed.

9. The first flexor of the fore wing originates from the posteroventral part of the pronotum in Scelionidae and Vanhorniidae, whereas the muscle originates from the mesopleuron in all other Hymenoptera. The netrion apodeme limits anteriorly the site of origin of the first flexor of the fore wing.

10. Three type of netrion are described on the basis of the relative position of the netrion apodeme and the posterior pronotal inflection.

11. The oclucor muscle apodeme is absent in basal Scelionidae, and the muscle originates from the pronotum with fan shaped origin. In *Nixonia* the muscle originates posterior to the netrion apodeme.

12. The skaphion apodeme crosses the site of origin of the longitudinal flight muscle.

13. The lateral and dorsal axillar surfaces and the axillar carina were defined and described first time in Platygastroidea.

14. The retractor of the mesoscutum is reported in Platygastroidea and the variability of the muscle and corresponding sceletal structures within the subfamily is described.

15. The term sternaulus is redefined on the basis of the site of origin of the mesopleuro-mesobasalare muscle.

16. The term speculum is adopted from Ichneumonidae and Cynipoidea taxonomy on the basis of the site of origin of the mesopleuro-mesofurcal muscle.

17. The remnants of the mesopleural ridge, sulcus and mesopleural arm and pit and the putative border between the mesepisternum and mesepimeron is discussed.

18. The mesopleural depressor of the mesotrochanter sensu Gibson (1985) originates from the anterior extension of the mesofurca and therefore the muscle is redefined and referred in the present study as the lateral mesofurco-mesotrochanteral muscle. In *Nixonia*, *Sparasion*, *Idris* and *Gryon* both the lateral and median mesofurco-mesotrochanteral muscles are present.

19. The mesofurco-mesotrochanteral muscle present in Platygastriidae.

20. The second flexor of the hind wing at least partly originates from the posteriorly delimited area of the mesopectus in Scelionidae similarly to some other Proctotrupoidea s.l. and Chalcidoidea. The serial analogy of this area and the netrion is discussed.

21. The homology of the medially elevated area of the metanotum (dorsellum) of apocritans and mesoscutellum and the possibility of the usage of the term metascutellum in Apocrita is discussed with the descriptions of correlating internal structures.

22. The anterior metanotal wing process is located on an independent humeral sclerite in Scelionidae.

23. The metanotal depressor of the metatrochanter originates from the humeral sclerite in Scelionidae as well as in some other Proctotrupoidea s.l.

24. Vilhelmsen (2000a, 2003) considered the anteriorly located metafurca on the metadiscal lamella to an autapomorphy for Hymenoptera. The metapleuron is extended secondarily dorsally of the metapleural ridge and corresponding metapleural sulcus in Scelionidae. In Telenominae, *Gryonini* and *Baeini* the metafurca is located posteriorly on the metadiscal lamella.

#### *World revision of Xenomerus Walker 1836*

With 466 species in 11 genera (Johnson 1992) Teleasinae is one of the largest and most common group of Platygastroidea, however, the limits of genera within the subfamily are not well-defined. One of the aims of our dissertation is to clarify the generic level concept of the genus *Xenomerus* on the basis of newly established morphological characters, based on the correlation of external and internal structures, such as internal apodemes, skeleto-musculature and gland systems (Mikó et al. 2007b). Beside this the author consider the present revision as a model for further revisions in Hymenoptera; based on the results of functional morphology. The Old World genus *Xenomerus* Walker is revised. As the result:

25. Thirty-eight species are recognized.

26. Three comb. nov. are established: *X. buccatus* (Kononova & Kozlov), comb. nov.; *X. calligetus* (Kononova & Kozlov), comb. nov.; *X. cornutus* (Kononova & Kozlov), comb. nov.

27. Four species are redescribed: *X. canariensis* Huggert, *X. ergenna* Walker, *X. laticeps* Dodd and *X. varipes* Dodd.

28. Twenty seven new species are described: *X. armatus* (Oriental), *X. aureipes* (Ethiopian), *X. bickeli* (Australian), *X. comatus* (Ethiopian), *X. darlingi* (Oriental), *X. fragilis* (Ethiopian), *X. fulleri* (Australian), *X. gloriosus* (Australian), *X. guinensis* (Australian), *X. halteratus* (Australian), *X. hilleri* (Australian), *X. feehani* (Ethiopian), *X. kalocsai* (Ethiopian), *X. madag* (Ethiopian), *X. malawi* (Ethiopian), *X. melikai* (Australian), *X. melleus* (Australian), *X. noyesi* (Oriental), *X. ochraceus* (Ethiopian, Oriental), *X. orientalis* (Oriental), *X.*

*paraorientalis* (Oriental), *X. rugifrons* (Oriental), *X. scutellatus* (Ethiopian), *X. spinosus* (Oriental), *X. vanharteni* (Ethiopian), *X. watshami* (Ethiopian), *X. yamagishii* (Oriental).

29. Two new synonyms are proposed: *X. canariensis* (= *Trimorus mutator* Kononova & Kozlov, syn. nov.), *X. ergenna* (= *Trimorus curtum* Kononova & Kozlov, syn. nov.).

30. An identification key is provided

31. Four species groups are proposed and diagnosed.

32. Relationships of *Xenomerus* within the Teleasinae and the monophily of the genus are discussed.

33. The presence of the acrosternal calyx (a secondary modification around the opening of a putative exocrine gland) is unique for Teleasinae. Its variability within Teleasinae and possible usage in species group characterization are discussed.

## ÖSSZEFOGLALÁS

Disszertáció fő témája a Scelionidae (Hymenoptera: Platygastroidea) család funkcionális morfológiájának elemzése külső és belső karakterek tárgyalásával, majd ez alapján a scelionida szisztematikában használatos morfológiai szakkifejezések újradefiniálása és alkalmazása a leíró taxonómiában.

### *Scelionidae morfológia*

Munkám során megpróbáltam új karaktereket keresni, melyek használhatók mind a leíró taxonómiában mind a csoport filogenetikai vizsgálataiban. A már meglévő terminusokat megpróbáltam összevetni más Hymenoptera családokban használt terminusokkal belső, kapcsolódó struktúrák alapján. A családban használatos szakkifejezések letisztázása mellett a fő célom az volt, hogy hozzájáruljak egy általános Hymenoptera morfológiai nyelvezet létrejöttéhez, ami nélkülözhetetlen a rend magasabb szintű taxonjai között fennálló filogenetikai kapcsolatok, homológiák rekonstruálásához. A disszertációban leírtam a scelionidák fejének és a mezoszómájának (tor+áltorszelvény) külső struktúráit, ezekhez kapcsolódó belső struktúrákat, valamint a fejbe és a torba található izmokat a csápok, szájszervek valamint a lábak belső izmai kivételével. Dolgozatomban tárgyaltam a leírt struktúrák jelentőségét a csoport filogenetikai kapcsolatainak letisztázásában. Munkám eredményeit a következőkben foglalom össze:

1. 229 új morfológiai karaktert neveztem meg és definiáltam. Ezek közül 84 volt új vagy módosított.

2. 67 izmot definiáltam és homologizáltam más darázs csoportokban már leírt izmokkal.

3. A cranio-antennális izom egy olyan csáptőt mozgató izom, ami a crániumról ered a Scelionidae családban. Ez a jelleg valószínűleg autapomorfia a Scelionidae családra nézve, hiszen más Hymenoptera csoportokban mind a három csáptőt mozgató izom a tentóriumról ered.

4. Scelionidákban az episztómális barázda és a hozzá kapcsolódó belső episztómális taréj a szájnyílás első szegélyéig húzódik, a clypeo-pleurosztómális vonal hiányzik, a tentórium első fele összeolvad a rágó pleurosztómális ízesülési helyével. Ez a jelleg valószínűleg autapomorfia a Scelionidae családra nézve, hiszen más Hymenoptera taxonokban a tentórium jól láthatóan a szájnyílás első szegélye felett csatlakozik a crániumhoz.

5. A homlok-szirt olyan Scelionidae nemekben van jelen, ahol a rágó első ízesülési helye a szájnnyílás oldalára tolódik. A homlok-szirt a rágó távolító izmának tapadási helyét jelöli, ami a homlok-szirttel rendelkező nemekben a pófáról a homlok felső részére helyeződött át. Ez a másodlagos módosulás a rágó mozgásával és valószínűleg a darazsak életmódjával van összefüggésben.

6. A pharynx előrevonó izma a csáp ízesülési helyéhez képest dorzálisan ered a crániumról. Ez szintén a Scelionidae család autapomorfiájának tekinthető, mert az összes többi Hymenoptera csoportban az izom a csáp ízesülési helyéhez képest ventrálisan ered.

7. Scelionidáknál a szájnnyílás és az occipitális nyílás közötti másodlagos szklerotizáció genális eredetű, ezért ezt a terület homológ a levéldarazsak postgenális hídjával.

8. Scelionidákban a propleurális kar redukálódott, ezért azoknak az izmoknak a tapadási helyei, amelyek az összes egyéb darázscsoportban a propleurális karhoz csatlakoznak más, propleurális struktúrára helyeződtek át. A profurcális híd hiányzik a scelionidákban.

9. Az első szárny első hajlító izma scelionidákban valamint vanhorniidákban a pronótumról ered, míg az összes többi darázscsoportban az izom a mezopleuronról ered. Az izom tapadási helyét előlről a netrion apodéma határozza meg.

10. A netrion három típusát különböztettem meg a netrion apodéma és a hátsó pronótális hajlat egymáshoz viszonyított helyzetére alapján.

11. Bazális scelionidákban a pronótális spiráculum záróizom apodémája hiányzik, a legyezőszerű eredési hellyel rendelkező pronótális spiráculum záróizom közvetlenül a pronotum belső felületéről ered. A *Nixonia* nemben más scelionidáktól eltérően az izom a netrion apodémától poszterior ered.

12. A skaphion apodéma keresztezi a hosszanti indirekt repülőizom mezonotális tapadási helyét.

13. Az oldalsó valamint a felső axilláris régiókat és az axilláris karinát első ízben határoztam meg a Platygastroidea családsorozatban.

14. Kimutattam a mesoscutum visszahúzó izmának jelenlétét a Platygastroidea családsorozatban és tárgyaltam az izom és az eredési helyként szolgáló apodéma Scelionidán belüli variabilitását.

15. A sternaulust a hozzá kapcsolódó izmok alapján újradefiniáltam.

16. Az Ichneumonoidea és Cynipoidea családsorozatokban használatos speculum terminus használatát javasoltam a scelionidák mezopleuronjának felső, kívülről konvex régiójának elnevezésére, mert ez a mezopleuro-mezofurcális izom tapadási helyét szolgálja.

17. Megvitattam a belső mezopleurális taréj és mezopleurális apodéma, valamint a

velük összefüggő külső mezopleurális barázda és bemélyedés maradványának lehetséges helyét és ezek alapján a mezepisternum és mezepimeron határának meghatározhatóságát.

18. Kimutattam, hogy Gibson (1985, 1999) által mezopleurális eredetűnek meghatározott mezotrochanter mezopleurális visszahúzó izom valójában a mezofurca első kiszélesedő nyúlványáról ered minden olyan Hymenoptera taxonban, amely rendelkezik ezzel az izommal. *Nixonia*, *Sparasion*, *Idris* és *Gryon* nemekben mind a laterális, mind pedig a mediális furcális visszahúzó izom megtalálható.

19. A mesotrochanter oldalsó furcális visszahúzó izom (mezotrochanter mezopleurális visszahúzó izom sensu Gibson (1985, 1999)) jelenlétét először mutattam ki a Platygastriidae családban.

20. Kimutattam, hogy a scelionidákban valamint tágabb értelemben vett proctotrupeoideákban a chalcidoideákhoz hasonlóan a hátsó szárny második hajlító izma legalább részben a mezopleuron hátsó részéről ered. Megvitattam az elülső, valamint a hátsó szárny hajlító izmainak tapadási helyéül szolgáló, belső taréjjal leválasztott, pro- valamint mezopleurális régióknak (netrion és poszterior mezepimerális régió) szeriális analógiáját.

21. Kapcsolódó belső struktúrák alapján kimutattam, hogy a levéldarazsak metascutelluma valamint az apocriták dorselluma egymásnak homológiai és javasoltam a metascutellum terminus használatát a dorsellum helyett apocritákban.

22. A hátsó szárny első axilláris szkleritjének ízesülési pontja a metanótumtól elszeparálódott humerális szkleriten található Scelionidákban.

23. Első ízben mutattam ki a metatrochanter metanotális visszahúzó izmának jelenlétét a darazsak rendjében. Az izom a humerális szkleritről ered scelionidákban valamint más tágabb értelemben vett proctotrupeoideákban.

24. Vilhelmsen (2000a, 2003) szerint a metafurca az összes Hymenoptera-ban a diszkrimenális lamella első eredési helyétől ered, és ez a Hymenoptera rend autapomorfiájának tekinthető. Kimutattam, hogy a metafurca a diszkrimenális lamella hátsó feléről ered a Telenominae alcsaládban valamint a Scelioninae alcsalád *Gryonini* and *Baeini* nemzetségeiben.

#### *Xenomerus* nem világreviziója

A Teleasinae alcsaládba összesen 446 faj tartozik (Johnson 1992) és ezzel a fajszámmal a Scelionidae család egyik legnagyobb monofiletikus csoportjának tekinthető. A Teleasiane család képviselői általában nagyon gyakoriak, és szélesen elterjedtek. Bár a család monofiliája vitathatatlan, nemeinek határai nincsenek megfelelően meghatározva. Kutatásaim fő célja az

volt, hogy meghatározzam az egyik legrégebben leírt Teleasinae nem, a *Xenomerus* Walker 1836, generikus határait valamint elkészítsem fajainak világszintű revízióját.

A nem revíziójában olyan karaktereket és terminusokat használtam, amelyeket funkcionális morfológiai vizsgálataim során definiáltam (Mikó et al. 2007). A *Xenomerus* nem revíziója példa lehet arra, hogyan lehet a funkcionális morfológia eredményeit felhasználni a leíró taxonómiában. Munkám során a következő eredményeket értem el:

25. 38 *Xenomerus* fajt mutattam ki világszerte.

26. Három új kombinációt hoztam létre: *X. buccatus* (Kononova & Kozlov), comb. nov.; *X. calligetus* (Kononova & Kozlov), comb. nov.; *X. cornutus* (Kononova & Kozlov), comb. nov.

27. Négy, már leírt faj leírását adtam meg a fent említett morfológiai karakterek alapján: *X. canariensis* Huggert, *X. ergenna* Walker, *X. laticeps* Dodd és *X. varipes* Dodd.

28. 28 tudományra új fajt írtam le: *X. armatus* (Orientális), *X. aureipes* (Etióp), *X. bickeli* (Ausztrál), *X. comatus* (Etióp), *X. darlingi* (Orientális), *X. fragilis* (Etióp), *X. fulleri* (Ausztrál), *X. gloriosus* (Ausztrál), *X. guinensis* (Ausztrál), *X. halteratus* (Ausztrál), *X. hilleri* (Ausztrál), *X. feehani* (Etióp), *X. kalocsai* (Etióp), *X. madag* (Etióp), *X. malawi* (Etióp), *X. melikai* (Ausztrál), *X. melleus* (Ausztrál), *X. noyesi* (Orientális), *X. ochraceus* (Etióp, Orientális), *X. orientalis* (Orientális), *X. paraorientalis* (Orientális), *X. rugifrons* (Orientális), *X. scutellatus* (Etióp), *X. spinosus* (Orientális), *X. vanharteni* (Etióp), *X. watshami* (Etióp), *X. yamagishii* (Orientális).

29. Két új szinonimát ajánlottam fel: *X. canariensis* (= *Trimorus mutator* Kononova & Kozlov, syn. nov.), *X. ergenna* (= *Trimorus curtum* Kononova & Kozlov, syn. nov.).

30. Elkészítettem a nem világ szintű határozóját hímekre és nőstényekre.

31. *Xenomerus* fajokat négy fajcsoportba soroltam, melyeknek diagnózisát megadtam.

32. Tárgyaltam a *Xenomerus* nem monofiliáját valamint filogenetikai kapcsolatait más Teleasinae csoportokkal.

33. Kimutattam egy, a Teleasinae családra jellegzetes, metaszomális mirigyet, mely kivezető nyílása körül kialakult másodlagos kutikula módosulást felhasználtam fajcsoportok elkülönítésében.

## ACKNOWLEDGEMENTS

I am highly indebted to George Melika, my mentor and best friend, who showed me the interesting and challenging parts of hymenopterology and helped to find my way among so many difficult groups of wasps. His valuable comments and suggestions have always been helpful during my work. I would like to thank Lubomir Masner for his patience and willingness to answer my never-ending list of questions on Scelionidae. I feel lucky because I met him, and had the opportunity to work with him from the very beginning. I am also indebted to Zsolt Péntzes for many helpful discussions and suggestions during the course of this study. I would like to thank Gary A. P. Gibson and Lars Vilhelmsen who introduced me into the world of functional morphology; John Huber for advice in the descriptive morphology and preparatory techniques; and Henry Goulet for digital imaging techniques. I am highly appreciate the help of curators of many institutions (listed in APPENDIX 3).

Thanks to Mihály Földvári and Sándor Csósz (Natural History Museum, Budapest) who provided numerous great ideas during my research.

Also I would like to thank Norman F. Johnson who helped me with my scientific work and the preparation of the manuscripts.

I would like to thank my wife Vanda, my parents and my sister who helped me in many ways, and first of all they were patient enough towards my passion of working with wasps and muscles.

Financial support was provided by CANACOL (Department of Agriculture of Canada, Canadian National Insect Collection, Ottawa, Canada), HighLat (Naturhistoriske Riksmuseet, Stockholm, Sweden), NSF PBI (Ohio State University, Columbus, USA), Hungarian-British Intergovernmental Science and Technology Cooperation Programme (BMNH, London, UK), Hungarian-South African Intergovernmental Science and Technology Cooperation Programme (National Insect Collection, Pretoria, South Africa) and Synthesys (Natural History Museum, Copenhagen, Denmark).

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